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Circadian Rhythms of Locomotor Activity in Captive Birds and Mammals: Their Variations with Season and Latitude*

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Summary. 1. The seasonal variations in time of daily onset and end of locomotor activity are described for 3 species of mammals and 5 species of birds kept in captivity at the arctic circle and at lower latitude. These variations are most pronounced at high latitude.

2. The duration of daily activity plotted versus the photoperiod can be described as an *S*-curve in all species studied so far, both in nature and in captivity. In both male and female fringillid birds activity times were longer before the summer solstice (spring) than after the summer solstice at equal photoperiods.

3. The seasonal changes in activity time result from roughly mirror-image changes in the times of onset and end of activity relative to sunrise and sunset, cancelling out each other. Therefore the midpoint of activity stays relatively stable; remaining minor changes in the midpoint of activity do not produce a general seasonal pattern.

4. At high latitude, a large seasonal fluctuation in the day-to-day variability (or precision) of activity timing is detected. These patterns of precision of the rhythm cannot be attributed to a single Zeitgeber property without complex assumptions. Onset and ends of activity become more precise when occurring during the civil twilight, *i.e.* at times of day with most rapid changes in light intensity. This may reflect direct action of light on the rhythm rather than a property of the entrainment mechanism.

5. The data do not give compelling evidence for any formal model of the oscillations driving the activity rhythms. Predictions concerning the relation between phase and activity time derived from a single oscillator model are not matched by the data. On the other hand, the general seasonal patterns can be easily described in terms of a two-oscillator model.

6. Seasonal variations in duration of activity are larger in birds than in mammals. Day-to-day variations in timing are larger in mammals than in birds. The implications for photo-periodic time measurement are discussed.

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1. Introduction

The daily cycle of light and darkness is presumably the most powerful Zeitgeber entraining the endogenous circadian rhythms of plants and animals. Despite intensive research over the past decades, the mechanism by which the rhythm becomes entrained is still incompletely understood. Although it is not our main purpose to discuss the problems of entrainment in great detail, a few introductory comments on the principles involved are necessary.

Among different routes of action of a Zeitgeber one can theoretically distinguish between those which depend on its *differential* and *proportional* properties (Aschoff, 1960). With regard to the entraining mechanism, one can distinguish between *parametric* and *non-parametric* entrainment. The term "proportional" implies a continuous action of the instantaneous value of the Zeitgeber on the biological oscillation; if this affects one of the parameters of the oscillation, especially its angular velocity, the effect is per definition "parametric". In order to achieve entrainment by periodic alternations of proportional stimuli, a prerequisite is that the parametric effect changes with the phase of the circadian oscillation. In other words, for *parametric entrainment* there has to be a response curve of parametric effects, *i.e.* the difference between two values of angular velocity measured at two different light intensities has to be a function of the circadian phase. On the other hand, if there is no parametric entrainment but if there are nevertheless phase-independent effects on angular velocity measurable in constant conditions, proportional stimuli still could influence the "natural frequency" of an entrained circadian rhythm and hence indirectly determine the phase-angle difference between Zeitgeber and oscillation [for technical terms, see Aschoff *et al.* (1965) and also section 2.1]. In contrast to parametric entrainment, this will be called the *proportional effect*. *Non-parametric* entrainment is based on rather abrupt phase-shifts of the endogenous oscillation (instead of a continuous modulation of angular velocity); such phase-shifts are the result of differential stimuli of the Zeitgeber. As in parametric entrainment, a prerequisite for non-parametric entrainment is again that the magnitude of the phase-shifts is phase-dependent.

The possibilities for parametric or nonparametric entrainment, as well as for proportional effects depend on the properties of the daily light-dark (LD) cycle. Various characteristics of the LD cycle, its amplitude, the photoperiod and the duration of twilight vary systematically with season and latitude. The question can be asked to what extent seasonal and latitudinal variations in the behaviour of entrained circadian rhythms reflect common mechanisms in the action of the Zeitgeber. The seasonal changes in the natural LD cycle provide a wide array of "experimental conditions", especially at high latitude, although the combinations of photoperiod, twilight and amplitude, are not unlimited.

Apart from the mechanism of entrainment there is further reason for interest in seasonal and latitudinal patterns of entrained circadian rhythms. The recognition that circadian rhythms are involved in photoperiodic time measurement (Bünning, 1963) and in sun compass orientation (Kramer, 1950; von Frisch, 1950) clearly demands a thorough knowledge of general patterns of phase control as affected by season and latitude. For instance latitudinal variation in the phasing of circadian rhythms in birds migrating over large North-South distances should certainly affect the time compensation in sun compass orientation. And the small year-to-year variations in some of the biological phenomena presumably under photoperiodic control (for example the dates of arrival of migrating birds in spring, see Phillips, 1913) can only be understood on the basis of at least the same precision in phasing of the endogenous circadian oscillations involved in the measurement of photoperiod.

Locomotor activity of caged animals is among the easiest assays of circadian rhythmicity. In many species the natural activity is more or less restricted to either the light fraction (day-active species) or to the dark fraction of the cycle (night-active species). In such species, sharp onsets and ends of the daily activity often represent well-defined phase points of the rhythm. Yet, in conditions of entrainment they are not necessarily a reliable guide to phases of the "driving oscillation". Experimentally, one can elicit activity that is out of phase with the driving oscillation, a phenomenon called "positive masking" (Aschoff, 1960; Hoffmann, 1969). The possibility that to some extent masking—direct action of the light-dark-cycle, evoking activity or suppressing activity ("negative masking"), as distinct from its entraining effect on the underlying biological oscillation—occurs in natural conditions as well, should not easily be discarded. Yet, the systematic seasonal shifts of the daily onset and end of activity relative to given light intensities (Aschoff and Wever, 1962) strongly suggest that also in nature, both the onset and end of activity reflect internally defined phases of the driving oscillation rather than externally evoked responses. Locomotor activity can, then, be used as an appropriate indicator of phase of the endogenous rhythm. In this way, it has indeed been successfully applied to the study of circadian rhythms involved in sun-compass orientation (Hoffmann, 1960) and photoperiodic time measurement (Hamner and Enright, 1967).

Systematic seasonal trends in the timing of activity in birds have long been known (*e.g.* Schwan, 1920; Scheer, 1952; Franz, 1949). But it was not until a general model of circadian rhythms and their synchronization by light-dark cycles was developed that an attempt could be made to explain these variations on a general basis (Aschoff and Wever, 1962; Wever, 1962, 1963, 1964; Aschoff, 1969). This approach has been fruitful. In recent years many investigators (Blume, 1964, 1965; Corti, 1966; Dancker, 1966; Naik and Razack, 1967; Haarhaus, 1968; Bohnsack, 1968; Blase, 1971; Hoser, 1971; Voûte, 1972; Laufens, 1972) have made systematic field studies on timing of activity, especially in birds and bats, and attempted to explain the patterns found with help of theoretical properties of the circadian clocks involved. In a review covering most of the studies accumulated, it has been concluded that the patterns of phasing of bird activity found in nature can be attributed to variations in both photoperiod and duration of twilight (Aschoff, 1969). There were, however, a few cases that did not agree with

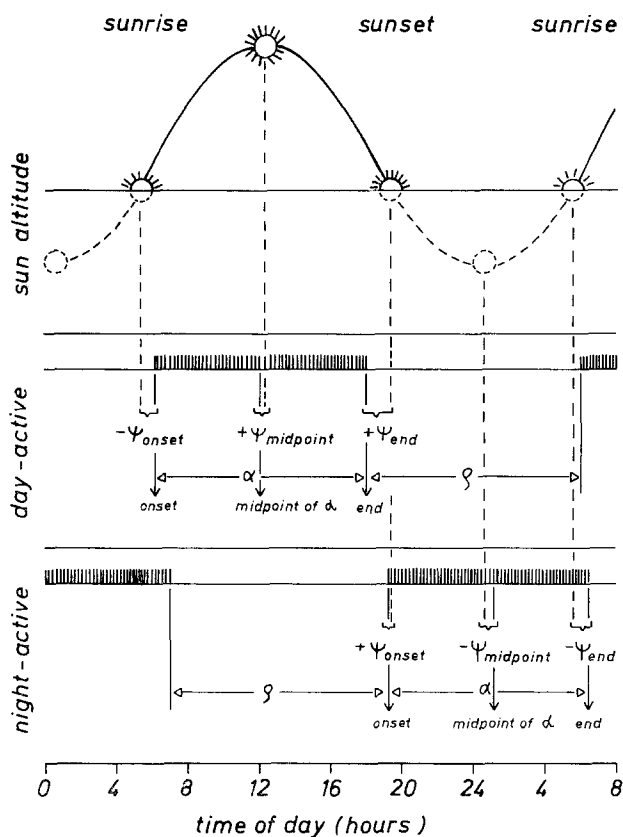


Fig. 1. Definition of onset and end of activity, phase-angle differences (ψ_{onset} , $\psi_{midpoint}$, ψ_{end}), activity time (α), and rest time (ρ) for day-active and night-active species

theoretical predictions. These were especially found among the few birds and mammals for which continuous activity records of captives were available at that time. This was one reason to extend the recording to further night-active and day-active species at different latitudes under natural light conditions both indoors (stabilized temperature) and outdoors. Since 1964, the activity of a large number of mammals and birds has been recorded at Erling-Andechs (47° 58' N, 11° 30' E) and later also at two research stations near the arctic circle in Sweden and Finland: Messaure (66° 42' N, 20° 25' E) and Oulanka (66° 27' N, 29° 21' E). Some of the results have been reported earlier (Aschoff *et al.*, 1970, 1972). The large material collected now allows a reconsideration of the effects of season and latitude on circadian activity rhythms.

The recording technique (event recorders) does not allow any statements on the amount of activity and its detailed temporal distributions, and the basic data analysed are only daily readings of onset and end of activity. Unfortunately, the analysis requires some unavoidable jargon. Greek symbols have been used to denote different time intervals characterizing the rhythms; and familiarity with the definitions is necessary for understanding this report (*cf.* Fig. 1 and Section 2.1.).

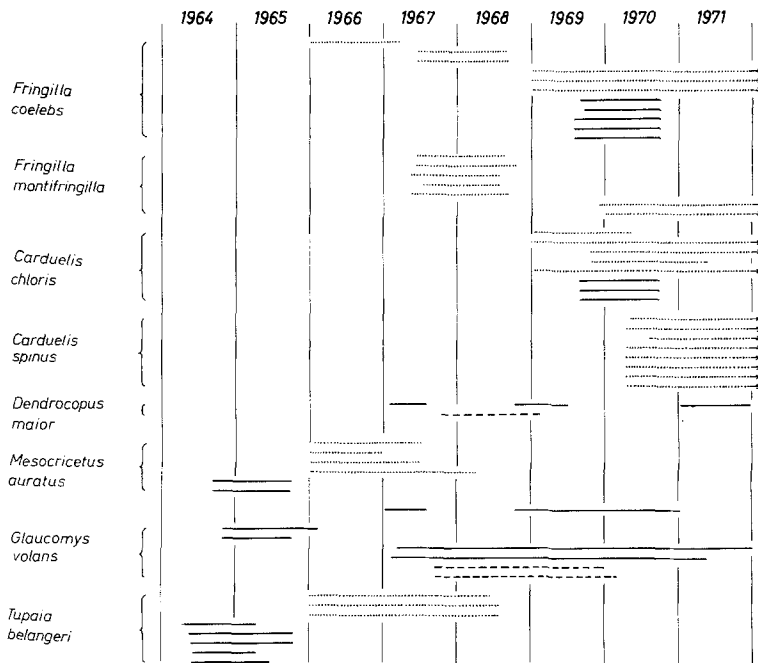


Fig. 2. Survey of records of locomotor activity analyzed in this report. Each horizontal line indicates the duration of a record for one individual, obtained in Erling-Andechs (solid lines), Messaure (dotted lines) or Oulanka (dashed lines)

2. Methodological Comments

2.1. Experimental and Analytical Procedures

In the present paper activity records from 57 animals, belonging to 5 species of birds (*Fringilla coelebs*, *F. montifringilla*, *Carduelis chloris*, *C. spinus*, *Dendrocopus major*) and 3 species of mammals (*Tupaja belangeri*, *Mesocricetus auratus*, *Glaucomys volans*), are analyzed. Details of the duration of each record are given in Fig. 2. Only records that lasted at least 6 months are included; many records covered 2 or 3 years.

Most birds and mammals were kept indoors. The birds were in cages with two perches, one of which rested on microswitches; the mammals were in cages with access to running wheels. The impulses elicited by perch-hopping or wheel revolutions were fed into separate channels of an event recorder. Examples of activity records of 4 species of finches in Messaure can be seen in Fig. 3 (for further examples see Aschoff *et al.*, 1970).

The outdoor recordings in Erling-Andechs and Oulanka were made in aviaries with 3 compartments housing a great spotted woodpecker, *Dendrocopus major*, and 2 American flying squirrels, *Glaucomys volans*, respectively. Each compartment was provided with a nest-box, accessible through a hole with a photocell-detector mounted in front. The habit of both species of spending their rest time in the nestbox was used in interpreting the data and, in most cases, onset and

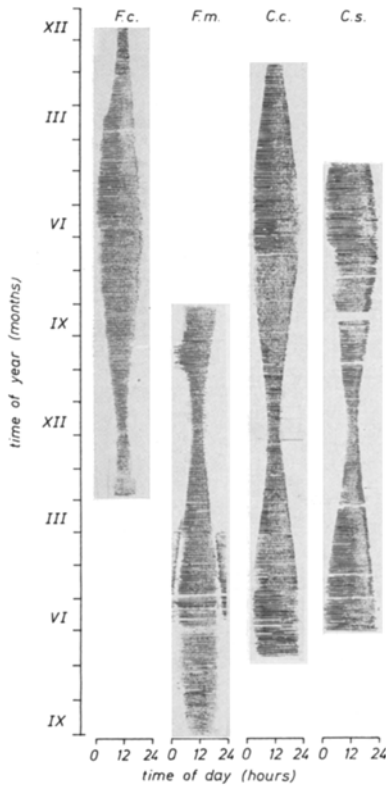


Fig. 3

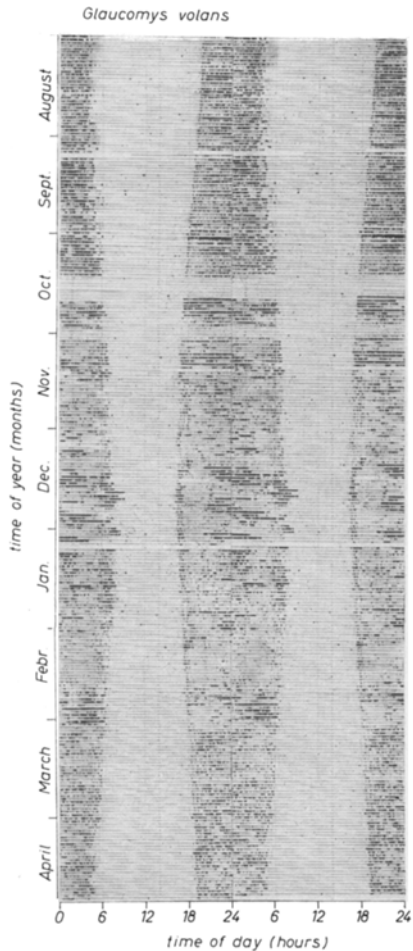


Fig. 4

Fig. 3. Examples of activity records of a chaffinch (*F.c.*), a brambling (*F.m.*), a greenfinch (*C.c.*) and a siskin (*C.s.*) in Messaure, Sweden. Each horizontal bar represents perch hopping activity of 1 day

Fig. 4. Example of an activity record of a flying squirrel in Erling-Andechs, as obtained by interruptions of a light beam in the entrance of the nestbox

end of activity could be unequivocally read from the records. An example of a flying squirrel record is shown in Fig. 4.

All experimental animals were given water twice or three times weekly and fed seed and pellet food, except for the woodpeckers which were given mealworms. The mammals additionally got lettuce and apples, and the tree shrews a newly hatched chicken from time to time. Onset and end of activity were read daily from all records. In seasons of nocturnal restlessness in the brambling (*Fringilla montifringilla*) only daytime activity was considered, and onset and end of activity

were measured only if daytime activity was clearly separated from night time activity (see Fig. 3).

Approximately 70000 readings of daily onset and end of activity, forming the basis of this paper, were fed into an IBM 1130 computer together with the year-round daily times for local sunrise and sunset as derived from the "Nautical Almanac". As units of "seasonal time" we have divided the year into 24 "half-months" [January 1-15, January 16-31, February 1-14, February 15-28 (29), etc.]. The first step in data reduction was the calculation of individual means and standard deviations over semimonthly (14-, 15-, or 16-day) intervals. This was done for the following parameters (see Fig. 1):

- onset of activity (local time);
- end of activity (local time);
- activity time α (in hours) = end—previous onset;
- rest time ϱ (in hours) = onset—previous end;
- phase-angle difference ψ (in hours):
- ψ_{onset} = sunrise—onset (day-active animals),
= sunset—onset (night-active animals),
- ψ_{end} = sunset—end (day-active animals),
= sunrise—end (night-active animals),
- $\psi_{\text{midpoint}} = 1/2(\psi_{\text{onset}} + \psi_{\text{end}})$.

In addition, the correlation coefficient r of ψ_{onset} and ψ_{end} was determined for each half month.

Examples of the seasonal variation of onset and end of activity, reduced to semi-monthly means and standard deviations, are shown in Fig. 5 for 4 individual animals. In many of the analyses described in subsequent sections species means and standard deviations were calculated as overall estimates from different individuals and different years. The term *photoperiod* is used for the light fraction of a day; when photoperiod is measured from sunrise to sunset it is called *sunlight*.

2.2. Estimation of the Course of Light Intensity

The activity records were collected without simultaneous registration of light intensity. Although this presents a serious handicap in interpreting the results, we can rely roughly on estimated daily curves of light intensity for some of the analyses. Such curves were obtained by calibrating computer-calculated daily curves of sun altitude using an empirical daily curve of light intensity.

The empirical curve (Fig. 6) was established with a photometer directed towards the zenith, protected from direct solar radiation and covered with neutral density filters when necessary, on a cloudless bright day in Erling-Andechs. Both the upper and lower limits of light intensity may be underestimated by the limitations of the equipment used. Similar curves obtained during twilight at other latitudes, at other times of the year, in different circumstances and with different equipment by Scheer (1952) and Hjorth (1968) compare well with the measurements (Fig. 6).

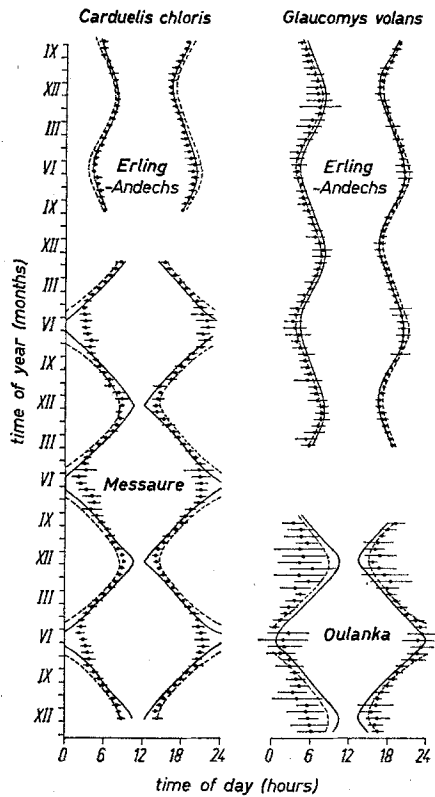


Fig. 5. Semimonthly mean daily onsets and ends of activity in a greenfinch (left) and in a flying squirrel (right), in Erling-Andechs (top) and at the arctic circle (bottom). Horizontal lines have a total length of 4 standard deviations. Solid lines show sunrise and sunset; dashed lines show times of beginning and end of civil twilight (sun 6° below the horizon)

Making use of a simplified formula for solar altitude, and of the calibrating curve, one can estimate daily curves of "zenith clear sky (zcs) light intensities" for any day of the year, and any place on earth. Four examples are shown in Fig. 7. For each of the locations, 24 curves were computed, estimating the course of zcs light intensity on January 8, January 23, February 7, February 21, etc., representing the middle days of the semimonthly periods.

It is obvious that bright, cloudless days are exceptional and that their frequency varies among localities on earth and between seasons. Furthermore, the experimental animals were never exposed to the same light intensity as the photometer directed to the zenith. The absolute values on the ordinate of such plots as Fig. 7 are therefore of no direct significance. It is, however, assumed that the *shape* of the calculated curves, plotted as they are in log units, approximates the *shape* of the daily curves of light intensity in the experimental rooms. This assumption is supported by incidental measurements (Fig. 8). Thus the semimonthly average light intensity to which an experimental animal was exposed

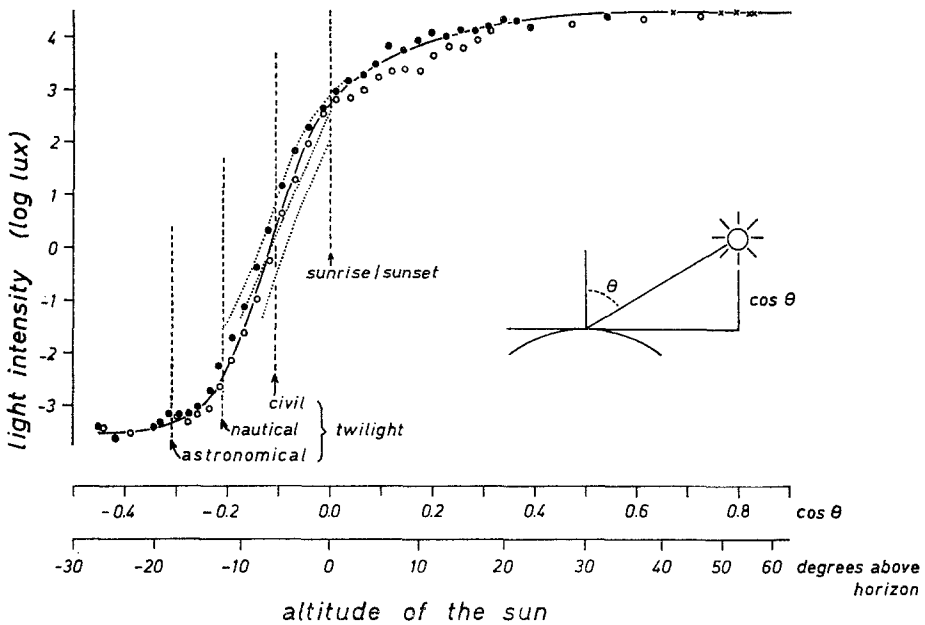


Fig. 6. Light intensity measurements taken at 10-min intervals on a clear day at Erling-Andechs (47°58' N, 11°30' E), plotted as a function of the altitude of the sun. Solid and open circles represent measurements in the evening of August 8, 1972, and in the morning of August 9, 1972, respectively. Crosses denote intensities beyond the capacity of the photometer used. The solid curve is eye-fitted. Dashed lines indicate time of onset of astronomical twilight (sun -18° from horizon), nautical (-12°) and civil twilight (-6°), and sunrise/sunset (0°). Of the 3 dotted lines, the middle one indicates measurements taken by Scheer (1952, Fig. 2) at 49°52' N, 8°39' E, while the outer curves are redrawn from the ranges of intensity measured by Hjorth (1968, Fig. 12) at 57°42' N, 14°28' E

at, say 7:00 a.m. is assumed to be a constant fraction of the calculated zcs light intensity for that semimonthly period at 7:00 a.m.

In the experimental room in Messaure, the time at which two twilight sensors (A and B) closed a circuit when the intensity of incident light rose above 4.5 lux (A; $\log \text{lux} = 0.7$) and 0.35 lux (B; $\log \text{lux} = -0.5$) respectively, was recorded on an event recorder during the experiments. From the average semimonthly times of those signals it was calculated that they operated at zcs light intensities (in $\log \text{lux}$) of:

$$\begin{aligned} &2.71 \pm 0.35 \text{ (A, morning),} \\ &2.49 \pm 0.27 \text{ (A, evening),} \\ &1.78 \pm 0.54 \text{ (B, morning), and} \\ &1.67 \pm 0.34 \text{ (B, evening).} \end{aligned}$$

The difference between real light intensity (0.7 and $-0.5 \log \text{lux}$, respectively) and zcs light intensity (averages from morning and evening) is then estimated at 1.9 (i.e., $2.6 - 0.7$) and 2.2 (i.e., $1.7 + 0.5$) log units by the two twilight sensors.

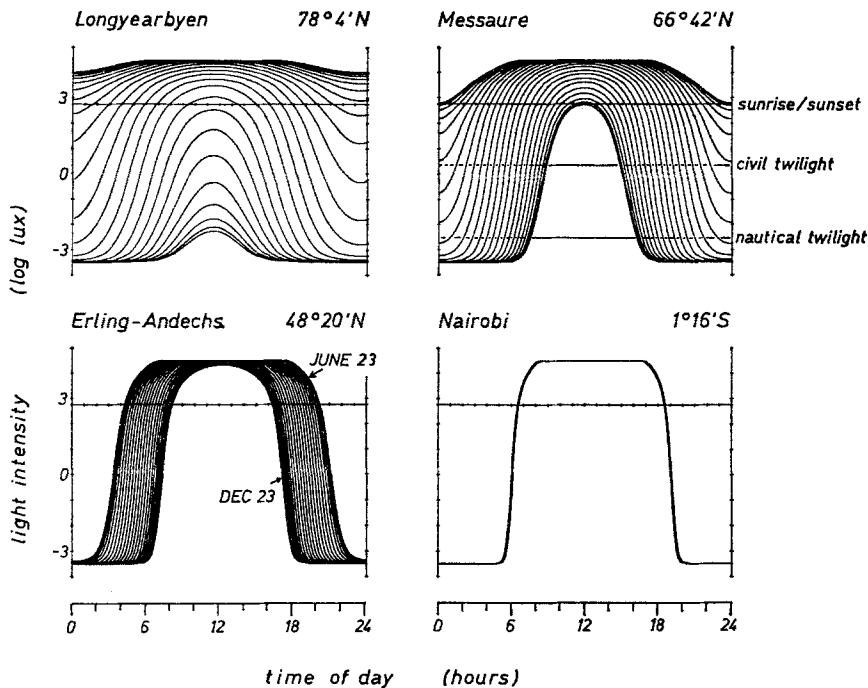


Fig. 7. Calculated curves of light intensity at the zenith under clear sky ("zcs light intensity") at 4 localities at different latitudes. The uppermost curves always represent June 23, the lowermost curves December 23. The curves between are for semimonthly midpoints. In the curves for Messaure, the zcs light intensities at sun altitudes of 0° , -6° (beginning or end of civil twilight), and -12° (nautical twilight) are indicated

Apparently, zcs light intensities were about two orders of magnitude larger than the real light intensities within the room. This estimate agrees again with the difference between the empirical curve and zcs curve in Fig. 8 (lower diagram). If the zcs light intensity curves gave an unbiased estimate of the average daily course of light intensity in the experimental room for any time of the year, the points in Fig. 9, indicating the zcs light intensity when the real light intensity had a fixed value of 4.5 lux (circles) or 0.35 lux (dots) should be distributed around horizontal regression lines. This condition is not entirely satisfied. At the same real light intensities in the experimental room, zcs light intensities were apparently slightly larger in midsummer (with the rising and setting sun in the north) than in midwinter (with the rising and setting sun in the south). Presumably, the exposure of the experimental room in Messaure to the southwestern sky, as well as the mountains in the northeast, have contributed to this effect. We believe that the difference is of minor importance, and that the zcs-light-curves give an estimate of the logarithmic rates of change of light intensity at different times of the day and the year valid for our purposes.

In Section 6, day-to-day variation in the timing of onset and end of activity will be discussed in relation to the estimated relative rate of change of light

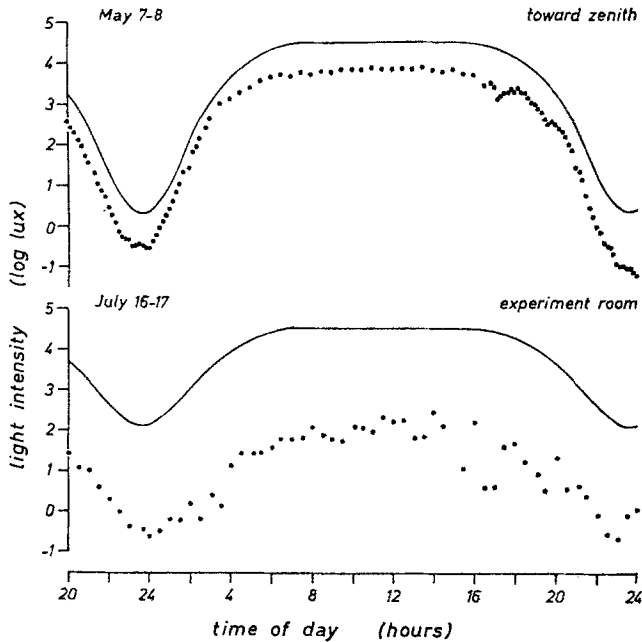


Fig. 8. Calculated "zcs light intensities" (solid curves) and light intensities measured (dots) on 2 days in Messaure in the summer of 1973. Measurements of light intensity with a photocell directed to the zenith (upper) and near the cages in the experiment room (lower). The sky was cloudy on both days

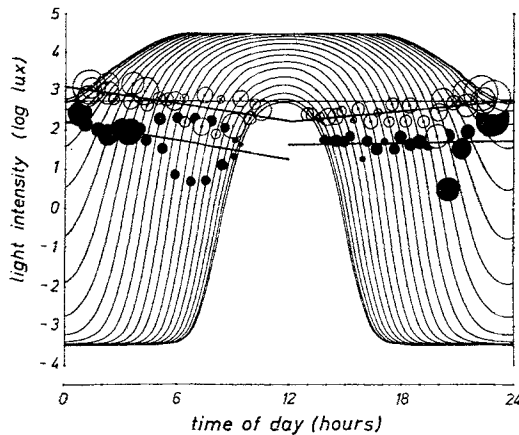


Fig. 9. Times at which two twilight sensors signaled light intensities in the experimental room in Messaure, together with the computed curves of "zenith clear sky" light intensities. The 24 drawn curves are taken from Fig. 7 (upper right panel). The mean times which the sensors measured light intensities of 4.5 lux (open circles) and 0.35 lux (closed circles) are shown for every half month on the appropriate zcs-light intensity curve. The radius of circles and dots is the semimonthly standard deviation of signal times. Thin horizontal line = zcs light intensity at sunrise or sunset. The 4 heavy lines are linear regressions through open and closed circles, respectively

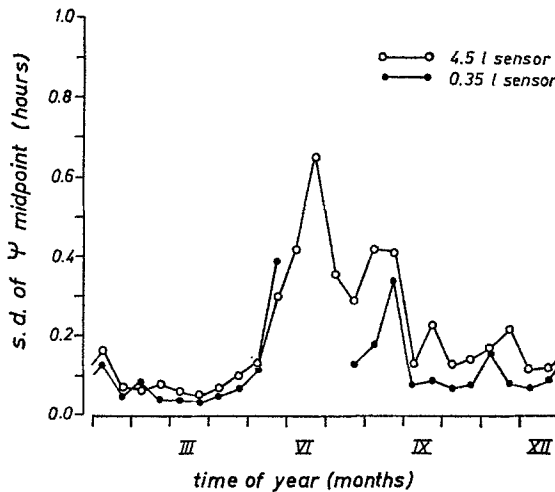


Fig. 10. Semimonthly standard deviations of the differences (ψ_{midpoint}) between the time of sun culmination and the midpoint of photoperiod, as measured from times at which two twilight sensors signaled light intensities of 4.5 and 0.35 lux respectively in the experimental room at Messaure. In June and in the first half of July, the light intensity in the room never were below 0.35 lux

intensity ($d \log I / dt$). It turns out to be of interest how a twilight sensor responding to a fixed light intensity rather than an internal clock entrained by periodic variations in light intensity, behaves in this respect. As can be inferred from Fig. 9, the light intensity threshold of 4.5 lux (*cf.* the thin horizontal line) in the experimental room is crossed by a much flatter part of the daily curve in summer than in other seasons. Day-to-day variations in cloudiness cause "vertical" scatter around the curve. "Vertical" scatter is transformed into "horizontal" scatter of the times at which a certain light intensity is surpassed on consecutive days by the slope ($d \log I / dt$) of the curve. Taking the standard deviations (s , circle radii in Fig. 9) of times at which the sensors operated for every half month, and the relative rate of change of zcs light intensity ($d \log I / dt$) at the average time at which the sensors operated, we find correlation coefficients between $1/s$ ("precision") and $d \log I / dt$ of:

0.35 (morning; $n = 24$; $P < 0.10$), and

0.45 (evening; $n = 24$; $P < 0.05$).

The rate of change of light intensity around the light intensity signalled by the sensors apparently is the cause of a seasonal variation in time precision of the switches (Fig. 10). Thus, when the sun moves at a small angle through the horizon, as happens in summer and winter, weather conditions such as cloudiness will have a relatively large effect on the time of day when a light intensity threshold is crossed. At the equinoxes, when the sun passes at a larger angle through the horizon, the time of a fixed light intensity is less affected by overcast, and thus less subject to day-to-day variations.

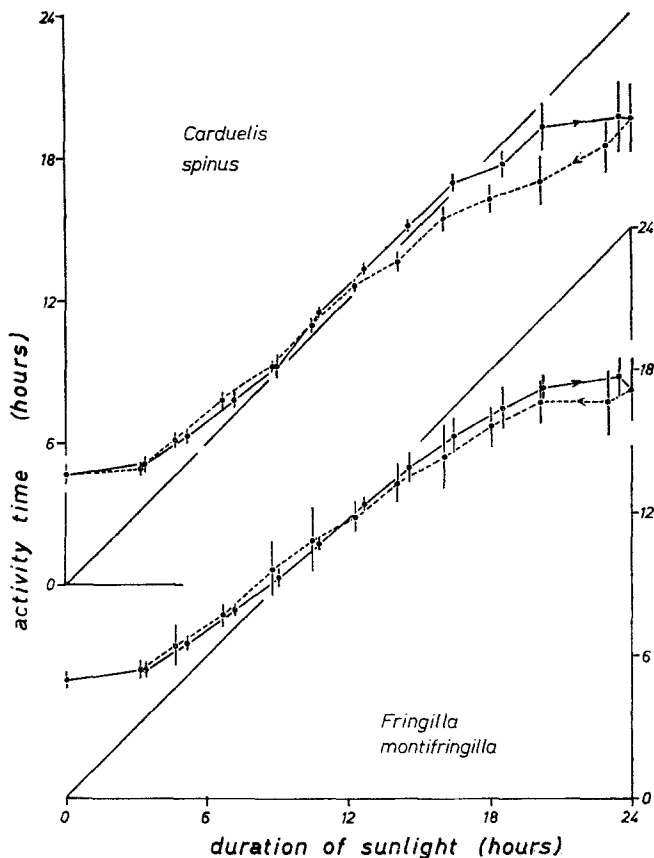


Fig. 11. Activity time as a function of sunlight duration in 8 siskins (top) and 7 bramblings (bottom) at Messaure, Sweden. Semimonthly interindividual means and standard deviations are shown. Solid lines: January-June; dashed lines: July-December. Arrows indicate the passing of time

3. Analysis of the Activity Records

3.1. Activity Time

Examples of the individual seasonal course of the onset and end of daily activity (Fig. 5) show that the activity time (α) follows the seasonal changes in duration of sunlight (greenfinches) or night (flying squirrels), to some extent but not completely. The relationships of α to the duration of sunlight (measured from sunrise to sunset) for all species studied are summarized in Figs. 11–15.

The 5 day-active bird species studied at the arctic circle (Figs. 11 and 12) have the S-curved relationship between α and sunlight duration as described earlier (Aschoff, 1969; Aschoff *et al.*, 1970). At days shorter than about 5 hrs, activity time is apparently independent of daylength. At intermediate daylengths (5–19 hrs), α increases rapidly, but the slope of the relationship is clearly less than 1. At very long days, the curve bends off again, and daylength does not

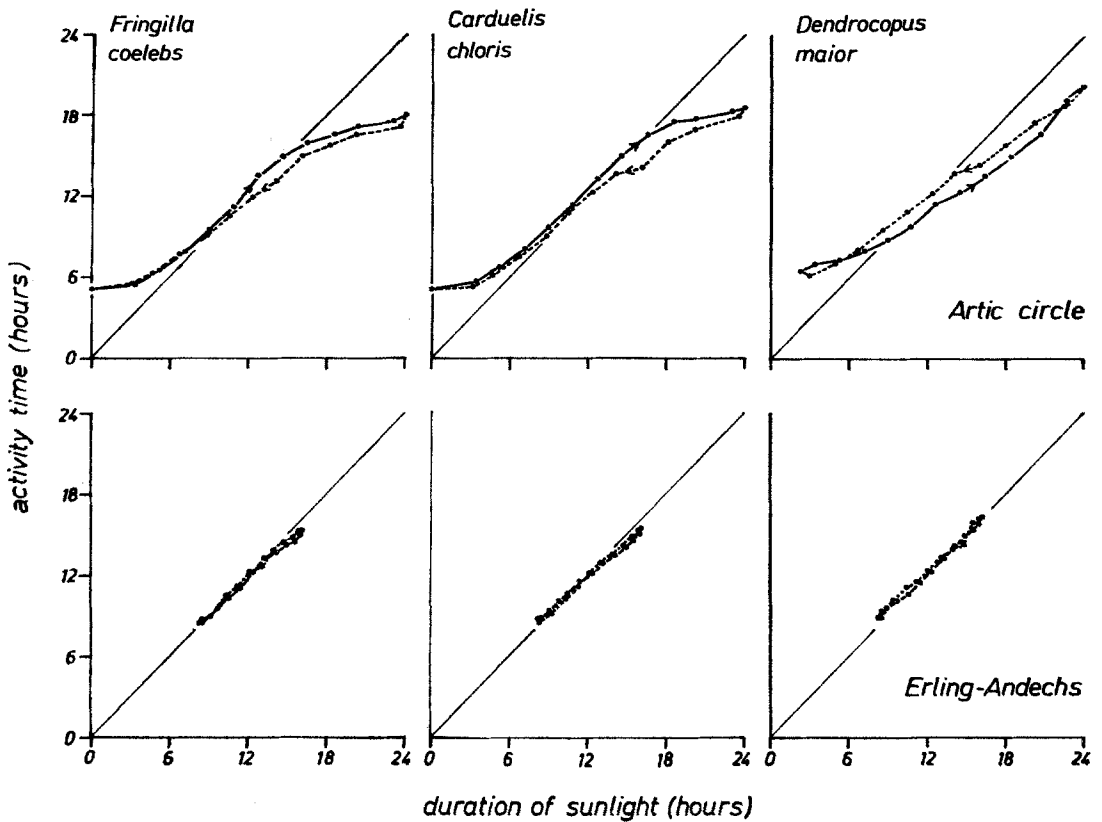


Fig. 12. Activity time as a function of sunlight duration in three species of birds at the arctic circle (top) and in Southern Germany (bottom). Semimonthly means from January to June (solid lines), and from July to December (dashed lines). Arrows indicate the passing of time

affect α when longer than about 19 hrs. The results obtained at lower latitude can be considered as a section from the intermediate range of sunlight durations (8–16 hrs) at higher latitudes. Similar S-curves were obtained by Aschoff (1969) in an analysis of field data from high latitudes on *Parus major*, *Emberiza citrinella* (both after Franz, 1949) and *Dendrocopos major* (after Blume, 1964).

At sunlights shorter than 12 hrs, no consistent differences between activity time in autumn and winter appear. In contrast, there is a general difference between activity times of the four species of finches, studied at Messaure, when equally long sunlights in spring and summer are compared. In these species, activity time is longer before than after the summer solstice at the same sunlight durations. In the siskins (*Carduelis spinus*), the difference in mean α between the second half of May and the second half of July was as large as 2.5 hrs. Activity records of captive warblers (*Phylloscopus collybita* and *P. trochilus*: Gwinner, unpublished results) as well as field data on another passerine bird (*Parus major*: see Aschoff, 1969; Fig. 12) show the same "hysteresis". On the other hand, the

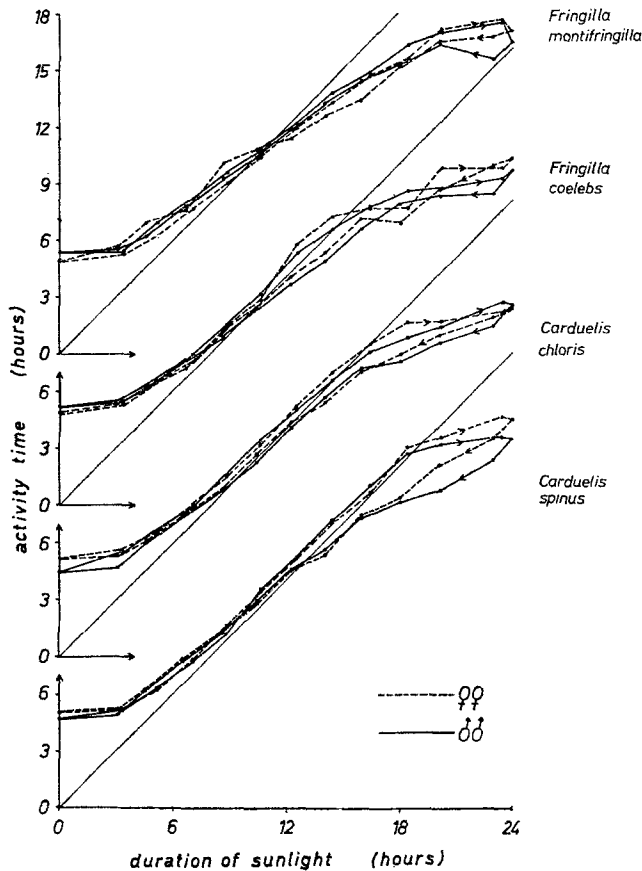


Fig. 13. Activity time as a function of sunlight duration in four species of finches at Messaure, Sweden. Sexes separate. Arrows indicate the passing of time

one great spotted woodpecker, studied in Oulanka, had a longer activity time after the summer solstice than before, in agreement with field data from this species at high latitude (Aschoff, 1969; Fig. 13).

The longer activity time of passerine birds in the spring than in summer at equally long sunlights, are presumably a result of endocrine influences relating to the reproductive state. In male starlings (*Sturnus vulgaris*), a positive correlation between testicular growth and activity time is known (Gwinner and Turek, 1971), and testosterone injections similarly induce an increase in α (Gwinner, 1974). The results obtained with fringillid birds at the arctic circle (Fig. 13) suggest such an endocrine effect for both males and females since in both sexes of all four species α is longer from April till June than from July till September. In spring and summer, females tend to have longer activity times than males. The larger α in the great spotted woodpecker (Fig. 12) after the summer solstice (dotted line) than before (solid line) may be related to the relatively later breeding season of this species (Glutz von Blotzheim, 1962).

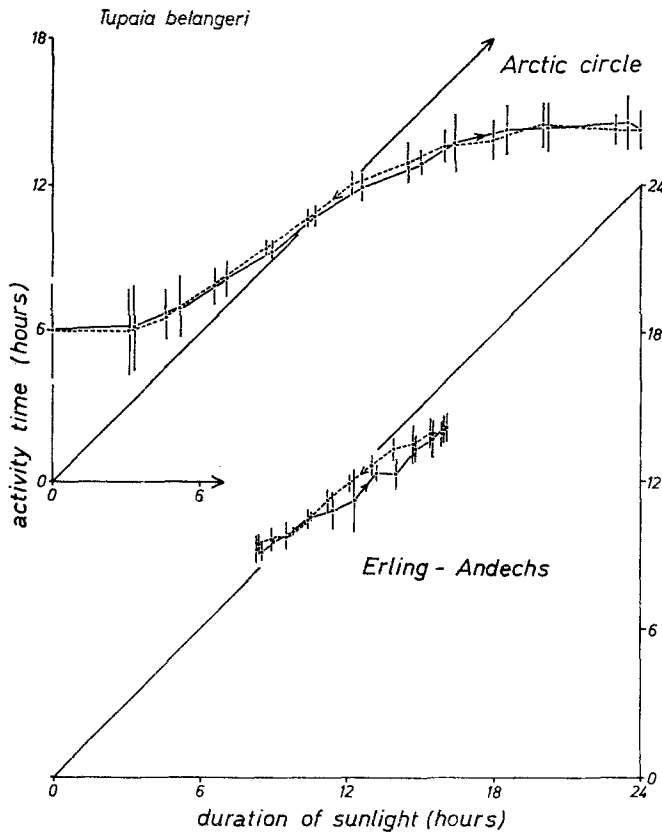


Fig. 14. Activity time as a function of sunlight duration in tree shrews, kept at Messaure (upper curve) and Erling-Andechs (lower curve). Semimonthly means and interindividual standard deviations are shown. Solid lines: Januar-June; dashed lines: July-December. Arrows indicate the passing of time

In the mammal species, a similar relationship of activity time to duration of sunlight (or night, respectively) is observed as in the birds (Figs. 14 and 15). The *S*-curves in the nocturnal hamster (*Mesocricetus auratus*) and flying squirrel (*Glaucomys volans*) are left-right reversed compared to Figs. 11-14; here activity time is negatively correlated with duration of sunlight. Again the results obtained in Southern Germany in all three species are in close agreement with those at equally long sunlights at high latitude.

A general difference between birds and mammals is that the curves of the mammals are less steep than those of birds, as previously reported (Aschoff, 1969). The range within which activity time changes with duration of sunlight, is smaller in mammals than in birds. A woodmouse (*Apodemus flavicollis*) recorded by Erkinaro (1970) in Northern Finland showed a dependence of α on sunlight duration similar to the curve of hamsters and flying squirrels.

When comparing activity time with sunlight duration one must recall that sunrise and sunset are arbitrarily chosen reference points of the daily light-dark

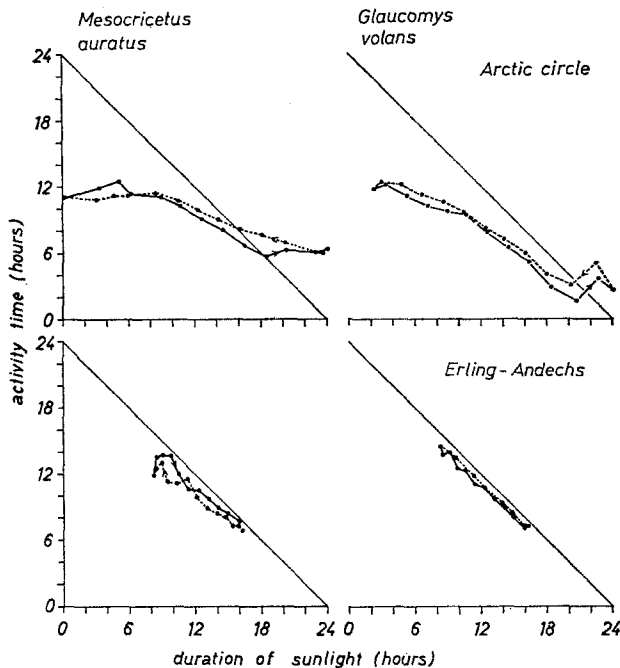


Fig. 15. Activity time as a function of sunlight duration in golden hamsters (left) and flying squirrels (right), kept at the arctic circle (top) and in Southern Germany (bottom). Solid lines: January-June; dashed lines: July-December. Arrows indicate the passing of time

cycle to determine photoperiod. One might expect a more consistent relationship between activity time and photoperiod, over the whole range of photoperiods, if instead of sunrise and sunset a certain angle of the sun below the horizon were taken to define photoperiod, for instance -6° (beginning or end of civil twilight) or -12° (beginning or end of nautical twilight). Plots of activity time as a function of these alternative measures of photoperiod are shown for some of the data from Messaure in Fig. 16. Neither of the two alternative transformations brings the mammal curves close to a 1:1 relationship between activity time and photoperiod. It is only in day-active birds (siskins) that the slope of the curve approaches 45° , at least for short winter days, when nautical twilight is included, but the activity time remains consistently shorter than the photoperiod. Thus, in none of the animals studied do the results support the conjecture that activity is limited by a fixed minimum solar altitude, below which darkness suppresses activity.

The general form of the dependence of activity time on duration of sunlight in captive animals fully supports the analyses of field data published earlier (Aschoff, 1969). The data again contradict ideas that activity time is directly determined by the presence of light within a range between some upper and lower limit of activity time set by physiological or ecological restrictions. Such considerations would explain a curve where sharp angles between the rising part and the flat extremes of the curve were found. The smooth form of the curves, as

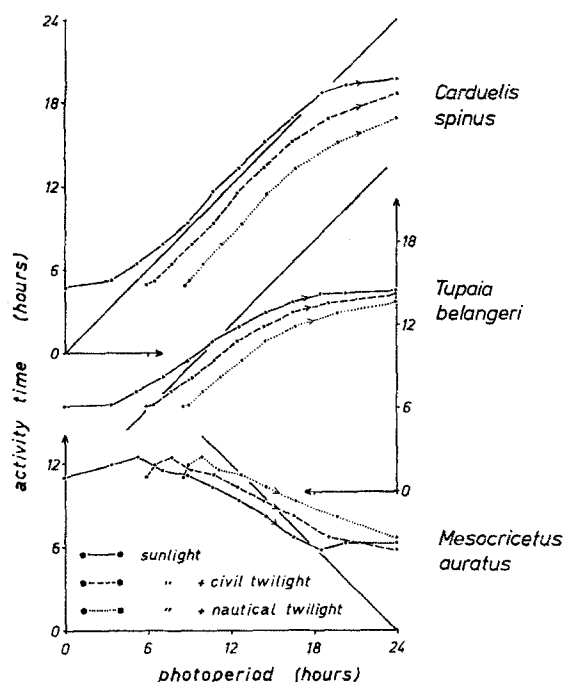


Fig. 16. Activity time in siskins (top), tree shrews (middle) and golden hamsters (bottom) at Messaure. The same data are plotted three times as a function of photoperiod measured either from sunrise to sunset (=sunlight duration) or including civil or nautical twilight. Only the data for the first half of the year (January to June) are shown. Arrows indicate the passing of time

well as the departure from 45° of the slope of the rising part, rule out such ideas. The general slope of the curves, even though subject to minor but significant variations, as between mammals and birds, and between spring and summer in birds, demands a general explanation in terms of the underlying timing mechanism. In Section 7, the general implications will be discussed in more detail.

3.2. Phase

3.2.1. Onset and End of Daily Activity

The analysis of activity time (α) as a function of sunlight duration in the previous section showed that α follows the seasonal variation only to a limited extent. This implies that the light intensities at which animals become active and terminate activity undergo significant changes in the course of the year. These seasonal trends are usefully illustrated by plotting the semimonthly mean times of onset and end of activity on the computed semimonthly curves of "ze-light intensity" (see Section 3). Examples of such plots are shown in Figs. 17 and 18.

Fig. 17 compares the results obtained with tree shrews (*Tupaia belangeri*) at high and low latitude. At the arctic circle (Messaure) there was apparently a

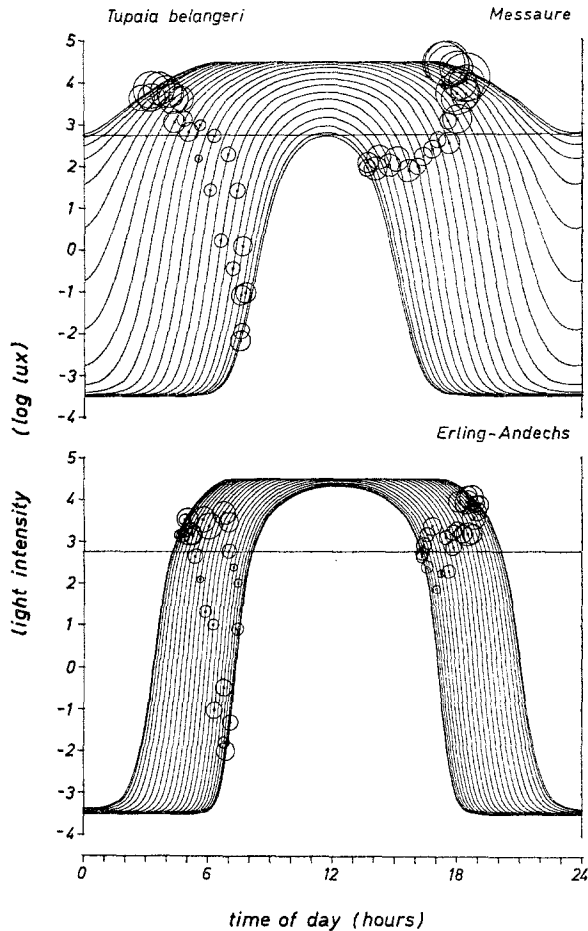


Fig. 17. Onset and end of activity in tree shrews kept at the arctic circle (top) and in Southern Germany (bottom), together with the computed curves for "zenith clear sky" light intensities. The 24 curves in each figure are computer constructed daily light curves for the middle days of the 24 halfmonths, as described in Section 2.2. The lowermost curve is for December 23, the upper-most curve for June 23. The horizontal line is at the light intensity for a sun position of 0° . Points on the curves indicate times of semimonthly mean onset (left) and end (right) of activity and "zcs" light intensities at these times. The radius of the circles is the standard deviation of the time of onset or end

decrease from summer to winter of 6 log units in the light intensity at which tree shrews became active. The end of activity occurred within a range of 2 log units. The results obtained in Southern Germany are a close match to those obtained in Messaure (Fig. 17, lower diagram). The light conditions at the arctic circle, covering a larger area of combinations of light intensity and time of day, seem better suited to reveal general principles.

Theoretically, it is possible that the daily onset and end of activity are completely exogenously determined by a particular threshold of light in-

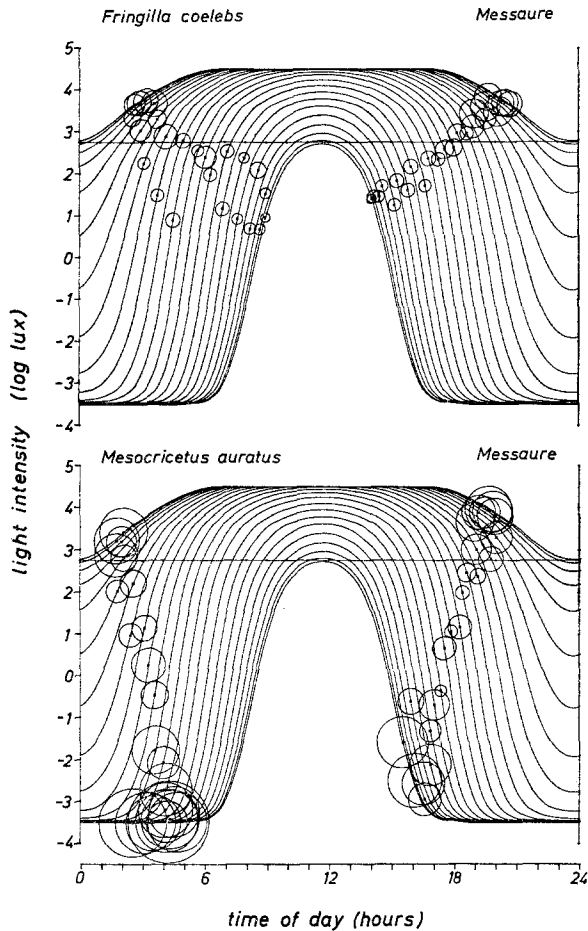


Fig. 18. Activity onset and end in chaffinches (top) and golden hamsters (bottom), together with the computed curves for "zenith clear sky" light intensities at Messaure. For conventions, see Fig. 17

tensity. An animal, in which this were the case, would show all onsets on a horizontal line, and all cessations on another horizontal line. On the other hand, a timing mechanism unaffected by light (but running with a period of 24 hrs) would produce all onsets and cessations vertically oriented in the light-intensity/time-of-day plane: at fixed local times. Apparently, the steepness of the slope by which mean onsets and ends of activity traverse the plane is suggestive of the influence light has on their timing. In the birds, these slopes are generally less steep than in the mammals studied. This is illustrated by the chaffinches and hamsters, studied in Messaure (Fig. 18), and by the linear regressions through mean onsets and ends of the 8 species studied in Messaure and Oulanka (Fig. 19). The timing of activity in the birds is apparently more influenced by light than in the mammals. In all regressions the slope is

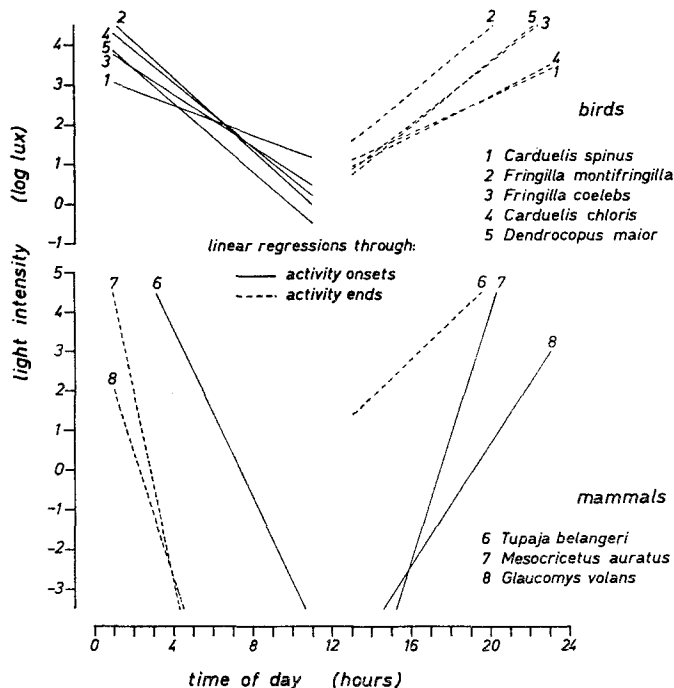


Fig. 19. Linear regressions of light intensity on time of day for activity onset and activity end in eight species kept at Messaure and Oulanka. For every species there are 2 regression lines: one for the onset of activity (solid line) and one for the end of activity (dashed line). Each pair was obtained from a graph such as those in Fig. 18

slightly steeper in the morning than in the evening, suggesting a slightly larger seasonal variation of light intensity at activity onset than at activity end in the day-active animals (night-active animals: smaller). But these differences are small, and given the approximative nature of the zcs-ligh-curves on which they are based, do not allow a firm conclusion.

It is both common and useful practice, in circadian literature, to relate onset and end of activity to characteristic phase points of the daily light-dark cycle, *e.g.*, sunrise and sunset. The time intervals separating the phase reference points of the activity rhythm and of the daily light-dark cycle are called ψ_{onset} and ψ_{end} (see Fig. 1). Figs. 20 and 21 show the seasonal course of the semimonthly means of both time intervals in the 6 species which were studied both at the arctic circle and in Southern Germany. In order to avoid such description of phase differences as "maximally positive" and "maximally negative" as have been used before we shall speak of maxima and minima and of large and small values of ψ , considering negative and positive values as a continuum.

The patterns found at high latitude are fairly homogenous: the day-active birds and tree shrews had their largest ψ_{onset} and smallest ψ_{end} in midwinter, smallest ψ_{onset} and largest ψ_{end} in midsummer. The changes in the night-active mammals are the reverse. Similar patterns are known from field data on *Emberiza*

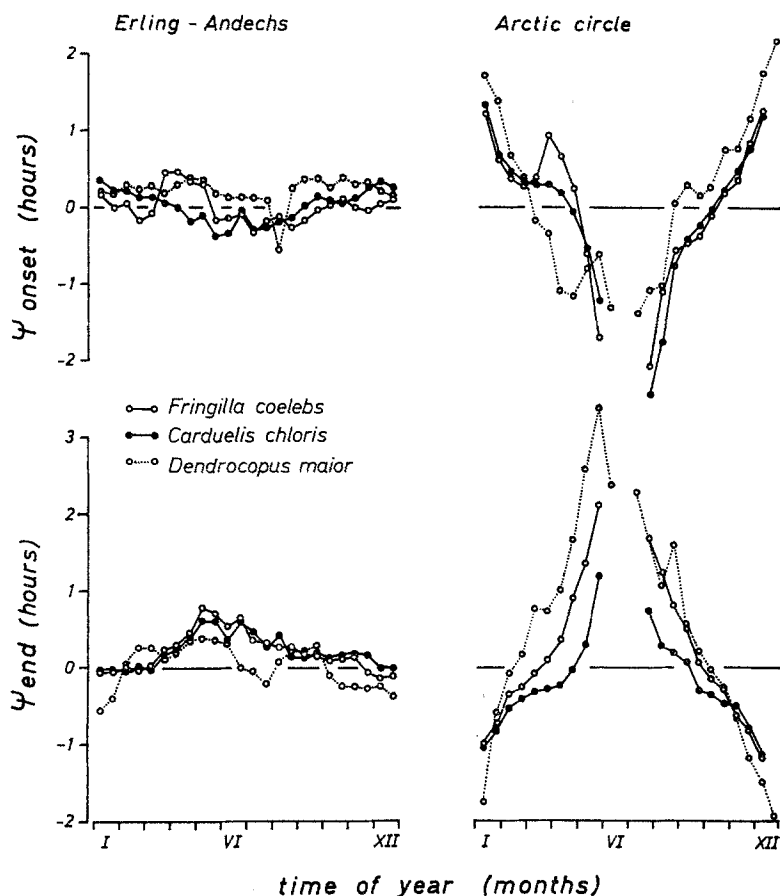


Fig. 20. Seasonal changes of ψ_{onset} , i.e., time of onset of activity expressed in hours before sunrise (top) and of ψ_{end} , i.e., time of end of activity in hours before sunset (bottom) in three species of birds in Southern Germany (left) and at the arctic circle (right)

citrinella, *Dendrocopus major* and *Erithacus rubecula* (see Aschoff, 1969; Figs. 8, 9 and 18). The mirror images of seasonal variation in ψ_{onset} and ψ_{end} are, of course, another expression of the change in light intensity at onset and end of activity discussed above. The differences at low latitude are much less pronounced than at high latitude, but for most species reveal the same seasonal tendencies.

A noteworthy departure from the general pattern is the sudden increase of ψ_{onset} in March in the chaffinches, both in Messaure and in Erling. This is in agreement with data for this species studied in Heidelberg (49°20' N), reported by Aschoff (1969; Fig. 23). It is apparently related to the general vernal maximum in activity time in fringillid birds (Section 4). A vernal reduction in the light intensity at which birds become active, necessarily implying and increase in ψ_{onset} , is known from several field studies (e.g., Scheer, 1952: *Turdus merula* and *Troglodytes troglodytes*; Hjorth, 1968: *Lyrurus tetricus*). Studies on the daily dis-

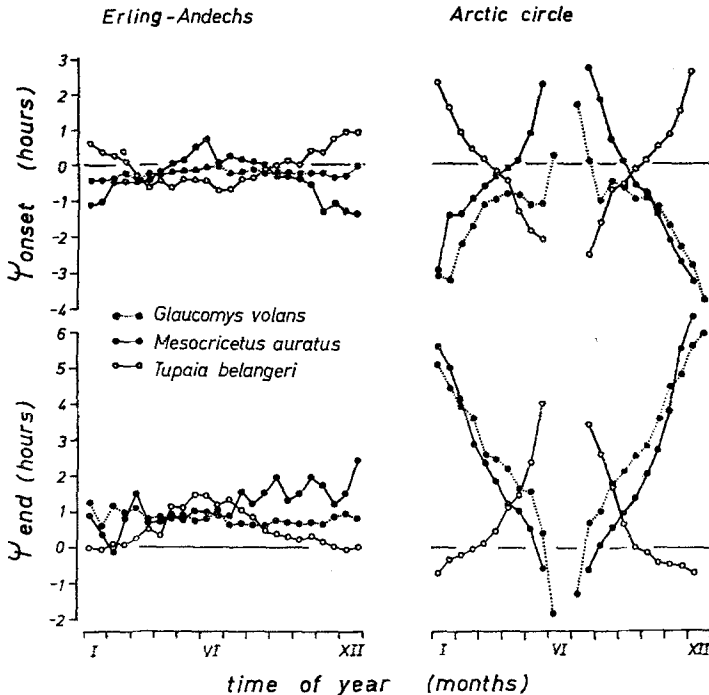


Fig. 21. Seasonal changes of ψ_{onset} (top) and ψ_{end} (bottom) in three species of mammals in Southern Germany (left) and at the arctic circle (right)

tribution of the amount of perch hopping activity revealed that the advanced onset of activity in spring is related to a large increase in the amplitude of the morning peak of activity (Daan, 1975).

It has been emphasized that the values of ψ_{onset} and ψ_{end} are of limited value in assaying the phase angle difference between activity rhythm and light-dark cycle (Aschoff, 1964, 1965). Apart from theoretical considerations, the argument was based on the heterogeneity of the seasonal changes in ψ_{onset} in different organisms. The data analyzed (Aschoff, 1965; Fig. 9) originated mainly from temperate latitudes, where seasonal changes in photoperiod are small. In such studies, changes in ψ_{onset} due to seasonal changes in the physiological state of the organism (*e.g.*, reproductive versus nonreproductive season) are likely to obscure the general trends, as suggested by the chaffinch results. At high latitude with large seasonal changes in photoperiod consistent general patterns in ψ_{onset} and ψ_{end} emerge.

3.2.2. Midpoint of Activity

A third measure of the phase angle difference between the activity rhythm and the entraining light-dark cycle is ψ_{midpoint} (Aschoff, 1965, 1969), *i.e.*, the time interval from midpoint of activity to sun culmination (in day-active animals) or to sun culmination + 12 hrs (in night-active animals) (see Fig. 1). A value of

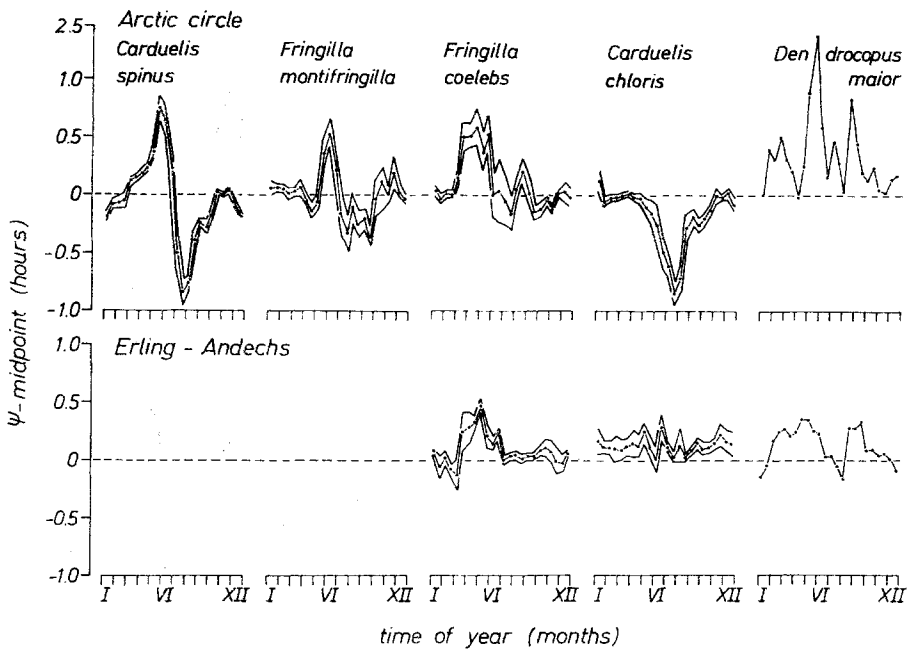


Fig. 22. Seasonal changes of ψ_{midpoint} (i.e., midpoint of activity time, expressed in hours before sun culmination) in 5 bird species kept at the arctic circle (top) and in Southern Germany (bottom). Enveloping curves connect points at a distance of 1 standard error from the semimonthly means (dots)

ψ_{midpoint} of +1 hr, for instance tells that the activity-time (α) phase leads the light-dark cycle by one hour, whereas a value of -1 hr means a phase lag by 1 hr. Since midpoint of activity and midpoint of rest are 12 hrs apart, a value ψ_{midpoint} of rest equals ψ_{midpoint} of activity. ψ_{midpoint} further equals the arithmetic mean of ψ_{onset} and ψ_{end} . As discussed above ψ_{onset} and ψ_{end} undergo roughly mirror-image seasonal variations, conspicuously so at high latitude. Their average, ψ_{midpoint} , therefore remains relatively constant, but shows the minor differences between the two in the absolute amount of change.

The seasonal course of ψ_{midpoint} in the species studied is illustrated in Figs. 22-24. With the exception of the three greenfinch records obtained in Southern Germany, all birds showed distinct seasonal changes (Fig. 22). The patterns are clearly species-specific.

Chaffinches (*Fringilla coelebs*) at both latitudes had maximal phase-angle differences in spring; and from about June to February, ψ_{midpoint} values fluctuated around zero. Greenfinches (*Carduelis chloris*) showed no regular changes in phase-angle differences in Erling-Andechs, but at the arctic circle they had their minimum ψ_{midpoint} in midsummer. Siskins (*Carduelis spinus*) in Messaure had a maximum phase lead in late spring (second half of May), then jumped backward to a 1-hr phase lag in the second half of July. Bramblings (*Fringilla montifringilla*) were rather erratic, but tended to have maximum phase leads in

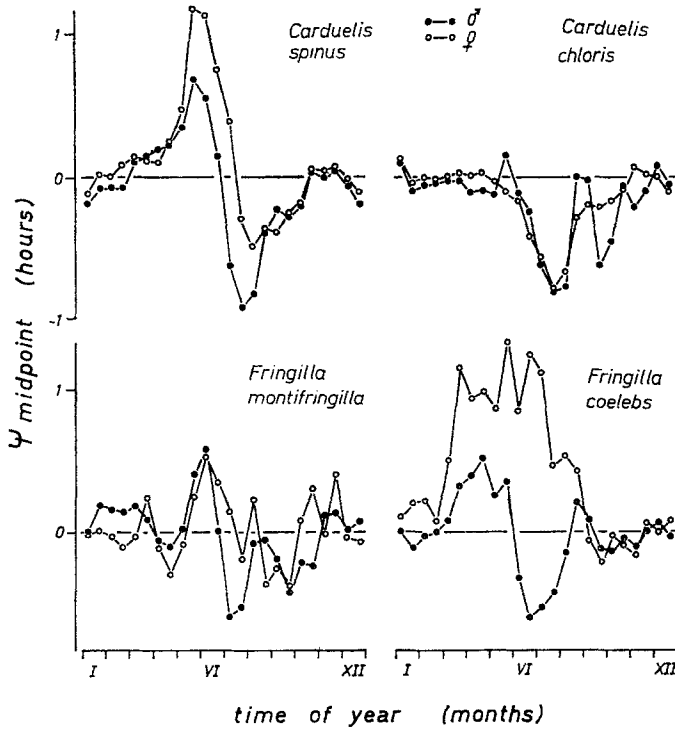


Fig. 23. Seasonal changes in ψ_{midpoint} in the 2 sexes of 4 species of birds in Messaure. Each point is the average for several animals and several years

May-June as well as in October-November, occurring more or less simultaneously with the periods of nocturnal restlessness (cf. Fig. 4). The data collected from two great spotted woodpeckers (*Dendrocopus major*) are not as complete as the finch records, but suggest maxima around May, both in Oulanka and Erling-Andechs (Fig. 22).

The feature common to the curves in all birds is the decrease of ψ_{midpoint} shortly before or around the summer solstice. A spring maximum is common to all but the Greenfinches. Fig. 23 confirms that males and females in the Messaure series had similar seasonal patterns of ψ_{midpoint} .

Among the mammals (Fig. 24) a clear seasonal pattern is absent only in the flying squirrels (*Glaucomys volans*) in Erling-Andechs. The 2 flying squirrels kept outdoors in the aviary for over 4 years, maintained a nearly constant phase lead of about 20 min throughout this period. In Oulanka, flying squirrels had a clear maximum phase lead in midwinter and a phase lag in midsummer. Golden hamsters (*Mesocricetus auratus*) also had maximum ψ_{midpoint} in midwinter in Messaure, but the 4 Erling animals showed too much interindividual variation to allow a firm conclusion. Tree shrews (*Tupaia belangeri*) at both latitudes had maximum phase lead in midsummer and a lower second maximum in midwinter. Minima in ψ_{midpoint} are found around the equinoxes, as described earlier (Aschoff, 1969; Aschoff *et al.*, 1970).

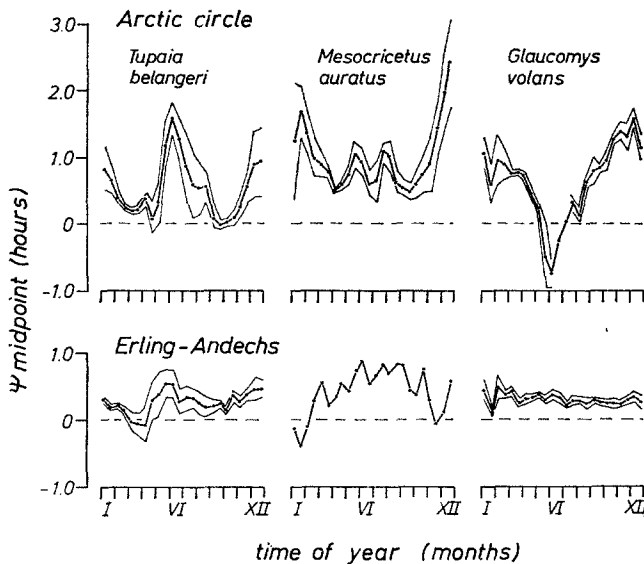


Fig. 24. Seasonal changes of ψ_{midpoint} in three species of mammals at the arctic circle (top) and in Southern Germany (bottom). Enveloping curves connect points at a distance of 1 standard error from the semimonthly means (dots)

The model for the influence of light on entrained activity rhythms, developed by Aschoff and Wever (1962), Wever (1962, 1963, 1964, 1965) and Aschoff (1965), makes some specific predictions on the seasonal changes in ψ_{midpoint} . The results presently discussed clearly have a bearing on these predictions. Assuming that the average light intensity in an LD-cycle affects the natural circadian frequency in the same way as it does in constant illumination (LL) (Aschoff, 1965, p. 270), and taking into account that an entrained oscillation phase-leads an entraining cycle increasingly more, the shorter its natural period (τ), the model qualitatively predicts that the phase-angle difference (ψ_{midpoint}) increases with photoperiod in species where τ decreases with greater intensity of constant illumination. Day-active birds have a negative, and night-active mammals a positive, dependence of τ on the light intensity in LL. The "seasonal rule" ("Jahreszeitenregel"), originally formulated by Aschoff (1964), states that the summer increase in photoperiod should result in an increased phase-angle difference (ψ_{midpoint}) in day-active animals and a decreased ψ_{midpoint} in night-active animals. Additional effects of the seasonal change in twilight duration, predicted by a mathematical formulation of the model (Wever, 1965, 1967), are such that an increase of ψ_{midpoint} in midwinter and midsummer, due to the long twilight, is superimposed on the yearly curve, and can produce a secondary maximum.

In the present results, only the seasonal change in ψ_{midpoint} of the mammals at the arctic circle can be described as a general pattern. A maximum is found in midsummer in the day-active tree shrews, in midwinter in the night-active golden hamsters and flying squirrels. Thus, unlike the birds, the mammals uniformly obey the original "seasonal rule". In the tree shrews, however, τ is positively

Table 1. Equinoctial phase-angle differences (ψ_{midpoint}) in southern Germany (Erling-Andechs) and at the arctic circle. Mean values and standard deviation are given in hours; numbers of original values in parentheses. P -values for the significance of difference between means were obtained with two-tailed t -test

Species	Erling-Andechs		Messaure/Oulanka	P
Second half of March				
<i>F. coelebs</i>	0.24 ± 0.36 (5)	<	0.50 ± 0.42 (12)	> 0.10
<i>C. chloris</i>	0.11 ± 0.12 (3)	>	0.01 ± 0.07 (12)	< 0.10
<i>D. major</i>	0.20 ± 0.06 (3)	=	0.20 (1)	—
<i>T. belangeri</i>	-0.17 ± 0.40 (5)	<	0.16 ± 0.17 (9)	< 0.05
<i>M. auratus</i>	0.19 ± 0.24 (2)	<	0.78 ± 0.30 (8)	< 0.05
<i>G. volans</i>	0.24 ± 0.11 (9)	<	0.75 ± 0.04 (3)	< 0.01
Second half of September				
<i>F. coelebs</i>	0.03 ± 0.09 (9)	>	-0.13 ± 0.24 (11)	< 0.10
<i>C. chloris</i>	0.15 ± 0.12 (5)	>	-0.25 ± 0.23 (9)	< 0.01
<i>D. major</i>			0.19 (1)	
<i>T. belangeri</i>	0.20 ± 0.11 (7)	>	-0.03 ± 0.11 (6)	< 0.01
<i>M. auratus</i>	0.44 ± 0.50 (2)	<	0.45 ± 0.23 (5)	> 0.10
<i>G. volans</i>	0.23 ± 0.13 (8)	<	0.83 ± 0.15 (5)	< 0.01

correlated with the intensity of constant light (Aschoff, 1969), and a maximum value of ψ_{midpoint} would be expected in midwinter rather than in midsummer.

Secondary maxima in the seasonal course of ψ_{midpoint} point occurred in the tree shrews in December, and in the golden hamsters in May and July, in agreement with the predictions from the model, and with earlier analyses of these data (Aschoff, 1969; Aschoff *et al.*, 1970). The presumed influence of twilight duration might further be expected to appear by comparison of ψ_{midpoint} observed around the equinoxes at different latitudes. Around the equinoxes, sunlight has nearly the same duration at all latitudes, but twilight lasts much longer at high than at low latitude. Table 1 summarizes the mean values of ψ_{midpoint} in the second half of March and the second half of September for the 6 species of which results are available both from the arctic circle and from Southern Germany. Significant ($P < 0.05$) differences between the 2 latitudes appear in 6 out of 10 cases. In 4 of these, ψ_{midpoint} is larger with the longer (arctic) twilight, in 2 it is larger at the shorter twilight (Southern Germany). Similarly, Aschoff (1969; Fig. 17) found no consistent dependence of equinoctial ψ_{midpoint} on latitude in the analysis of field data.

Thus, 2 of the mammals obey the seasonal rule, and the presence of 2 seasonal maxima in ψ_{midpoint} in the tree shrews and golden hamsters nicely confirms a prediction from the model. However, the seasonal and latitudinal variation in ψ_{midpoint} of flying squirrels, and especially the fact that all 5 bird species have different seasonal patterns of ψ_{midpoint} and none of them a pattern according to the rule, seem to refute the general validity of the model, when applied to conditions of natural daylight.

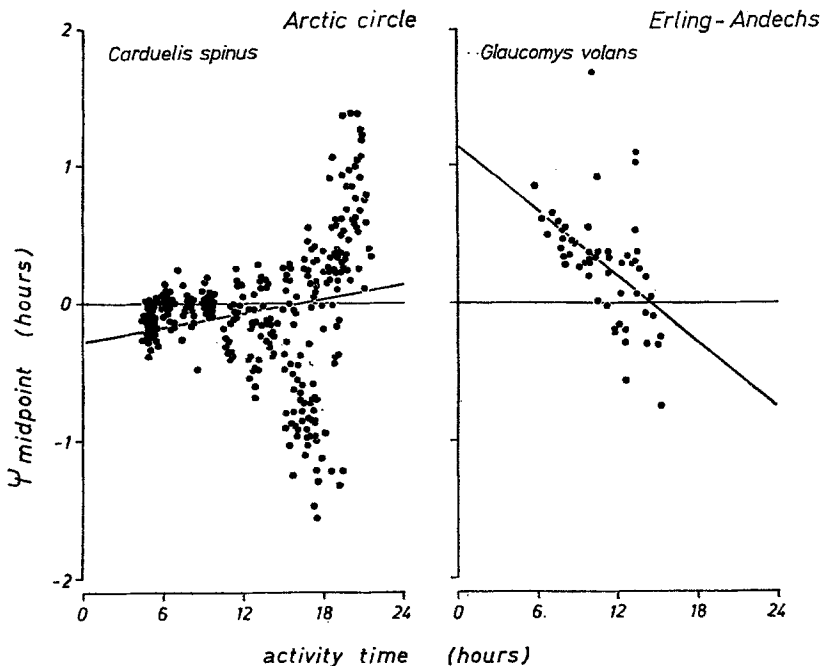


Fig. 25. Relationship between activity time and phase-angle difference in two species. Each dot represents a semimonthly mean α and its corresponding ψ_{midpoint} . Lines are linear regressions

Another aspect of the model is the coupling between the frequency and the mean level of the oscillation which in combination with a threshold, is responsible for timing of activity. Since the level is supposed to be reflected in the activity time (α), and the (natural) frequency (under entrained conditions) in the phase angle difference (ψ_{midpoint}), the most general prediction of the model is a positive correlation between α and ψ_{midpoint} , irrespective of the photoperiod.

The relationship between ψ_{midpoint} and α was analyzed by the calculation of linear regressions and coefficients of correlation between all semimonthly pairs of individual averages of ψ_{midpoint} and α . Two examples are shown in Fig. 25, and correlation coefficients for all experiments appear in Table 2. In 9 out of 15 cases, the regressions of ψ_{midpoint} on α had a slope significantly different from zero: 5 had a positive slope and 4 had a negative slope ($P < 0.01$). The results do not allow a general statement about the correlation (and hence the coupling) between the two parameters.

In summary then, the activity records obtained in natural day-light at different latitudes support the predictions derived from the model to a very limited extent only. Either too many other factors not accommodated in the model are involved, which differ from species to species and from season to season, and thus obscure general tendencies; or some of the basic assumptions—predictability of the effect of light on the “natural” frequency in entrained conditions based on its effects on the freerunning rhythm; internal coupling of level and frequency; usefulness of the midpoint of activity as phase reference point—are wrong. Else-

Table 2. Coefficients of correlation of phase-angle differences (ψ_{midpoint}) and activity time (α). Coefficients differing significantly from zero ($P < 0.01$) appear in bold type. The number of semimonthly means of ψ_{midpoint} and α compared is shown in parentheses

Species	Erling-Andechs	Arctic circle
<i>F. coelebs</i>	0.33 (154)	0.18 (291)
<i>F. montifringilla</i>		0.08 (233)
<i>C. chloris</i>	-0.13 (78)	- 0.40 (253)
<i>C. spinus</i>		0.18 (324)
<i>D. major</i>	0.20 (51)	0.44 (33)
<i>T. belangeri</i>	0.01 (138)	0.11 (180)
<i>M. auratus</i>	- 0.76 (50)	0.04 (145)
<i>G. volans</i> outdoors	- 0.18 (187)	0.70 (80)
<i>G. volans</i> indoors	- 0.50 (53)	

Table 3. Mean values of the semimonthly correlation coefficients of ψ_{onset} and ψ_{end} . The number of r -values contributing to the mean appears in parentheses

Species	Arctic circle	Erling-Andechs
<i>Carduelis spinus</i>	-0.17 (262)	
<i>Fringilla montifringilla</i>	-0.11 (184)	
<i>Fringilla coelebs</i>	-0.10 (241)	+0.07 (155)
<i>Carduelis chloris</i>	-0.16 (216)	+0.05 (79)
<i>Dendrocopus major</i>	-0.01 (33)	
<i>Tupaja belangeri</i>	-0.07 (151)	+0.03 (139)
<i>Mesocricetus auratus</i>	-0.01 (123)	-0.14 (87)
<i>Glaucomys volans</i> outdoors	-0.03 (87)	-0.06 (189)
<i>Glaucomys volans</i> indoors		-0.05 (54)

where (Daan, 1975) results are presented which show that the effect of light intensity on ψ_{midpoint} of finches is of a sign opposite to that predicted from the effect of light intensity in constant light.

3.3. Precision

The precision of the entrained rhythm of activity is expressed by the converse of the day-to-day variations in its timing. The semimonthly standard deviation of ψ_{midpoint} (ψ_{m}) has been taken as a measure of this variability. Precision of phase is then defined as $1/\text{s.d. } \psi_{\text{m}}$.

There is some justification in assuming that variations of activity onset (ψ_{o}) and end (ψ_{e}) contribute equally to the standard deviation of ψ_{midpoint} . Since

$$\psi_{\text{m}} = (\psi_{\text{o}} + \psi_{\text{e}})/2$$

$$\sigma^2 \psi_{\text{m}} = (\sigma^2 \psi_{\text{e}} + 2 \cdot r \cdot \sigma \psi_{\text{o}} \cdot \sigma \psi_{\text{e}})/4$$

where r is the coefficient of correlation between ψ_{onset} and ψ_{end} . Values of r were estimated for each animal in every semimonthly interval by Pearson's coefficient of correlation of ψ_{onset} and ψ_{end} . The average species values of r are given in Table 3. Although slightly negative in most animals, r clearly tends to be close to zero. Therefore

$$\sigma^2 \psi_{\text{m}} = 1/4 \cdot (\sigma^2 \psi_{\text{o}} + \sigma^2 \psi_{\text{e}})$$

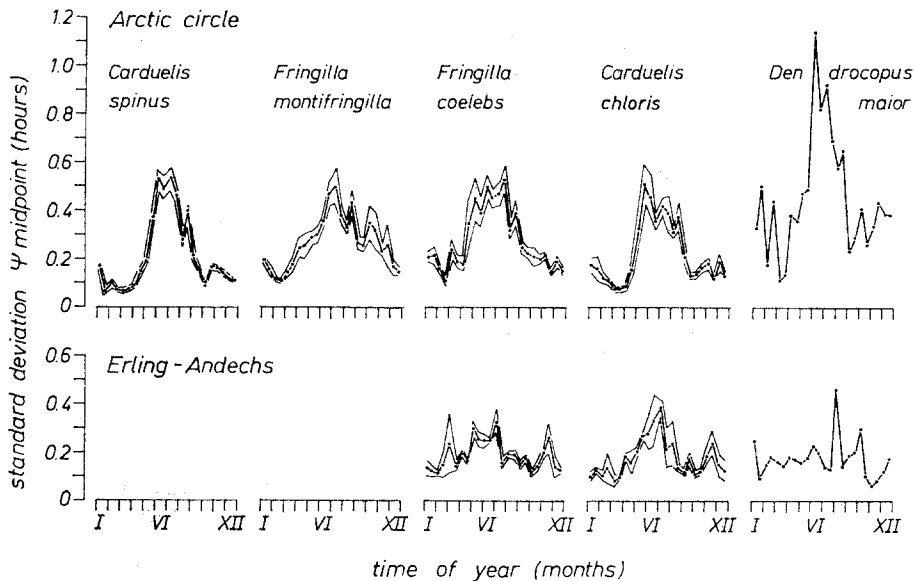


Fig. 26. Seasonal changes in variability of ψ_{midpoint} in 5 bird species kept at the arctic circle (top) and in Southern Germany (bottom). Enveloping curves connect points at a distance of 1 standard error from the mean standard deviation

is approximately correct, and the variances in activity onset and in activity end contribute equally to the variance of ψ_{midpoint} . It has to be pointed out here that the values of r (Table 3) are overall means for each species, averaged over long time spans. A more detailed analysis reveals a systematic seasonal trend in r . In the day-active siskins, for example, r tends to attain maximally negative values in December and January and is slightly positive in March and August. It could be tempting to discuss the compatibility of this pattern with the models discussed below (Section 4.2). However, the 2 twilight sensors (see Section 2.2) show seasonal changes of r similar to those of the siskins, and yearly averages of $r = -0.20$ and -0.28 . Therefore, the behaviour of r does not necessarily reflect a property of the driving oscillation.

The extent of variations in phase (or in precision) undergoes significant seasonal changes. An increase in variability of ψ_{midpoint} towards midsummer and towards midwinter has been reported by Erkinaro (1972) for the night-active owl *Aegolius funereus* and by Aschoff *et al.* (1972) for tree shrews and golden hamsters, all studied at high latitude. A summer increase in the variability of end of activity in greenfinches had already been observed by Palmgren (1943, p. 102). For the 8 species discussed here, Figs. 26 and 27 summarize the seasonal changes of the semimonthly standard deviations of ψ_{midpoint} . Significant seasonal fluctuations in variability are found especially in the results from the arctic circle. The 3 mammal species have a clear bimodal pattern, with larger variability in midwinter and midsummer than in spring and autumn. In the birds, variability is largest in summer, and the midwinter increase in variability is small, if present at all.

Clearly, there is a general seasonal trend in the variability of phase, particularly in the results obtained at high latitude. The difference in variation between the

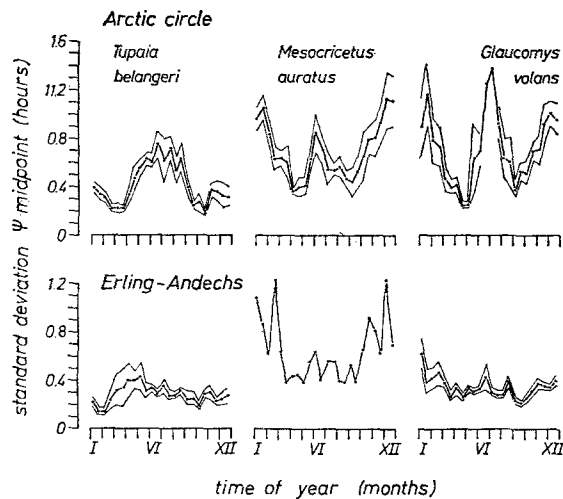


Fig. 27. Seasonal changes in variability of ψ_{midpoint} in mammals at the arctic circle (top) and in Southern Germany (bottom). Conventions as in Fig. 26

solstices and the equinoxes is in some cases as large as an order of magnitude. The question arises whether this change in variability indicates any specific property of the mechanisms involved in the timing of activity. There are 3 general sources from which variation in the timing of the observed activity could emerge: (1) the endogenous circadian rhythm, (2) the entrainment of this rhythm by the Zeitgeber, and (3) direct external influences on the overt rhythm. Explanations of the seasonal changes in precision can be derived from each of these 3 sources as follows:

(1) The endogenous clock can be assumed to be least precise around summer and winter solstices. Since some freerunning activity rhythms are most precise somewhere in the middle of their range of frequencies, *i.e.*, around $\tau = 24$ hrs (Aschoff *et al.*, 1971), one might presume that the "natural frequency" depends somehow on season and passes through this maximum-precision value twice a year, in spring and in autumn. Erkinaro's (1972) approach to the problem is of this type.

(2) It can be argued that phase control is better with stronger Zeitgebers, and that Zeitgeber strength decreases towards the winter and summer solstices.

(3) Direct action of light on the overt rhythm, producing either additional activity during the clock-determined rest time of an animal ("positive masking"), or partial suppression of activity during the activity time ("negative masking") (see Aschoff, 1960; Hoffmann, 1969). It could be argued that such masking effects are minimal in spring and autumn, due to the near coincidence of the mean activity onset and end with dawn and dusk.

All of these are complicated propositions, and it is likely that the seasonal change in variability is a result of more than one factor. (There are still more complicated conjectures about the seasonal variation in precision of entrainment,

related to the different slopes of phase-response curves for long and for short photoperiods, and with varying τ , to different daily phase-resets. We feel, however, that too little is known of these properties in the entrainment mechanism of our species to make further exploration of these conjectures presently fruitful.) From a further analysis of our results—obtained in natural daylight, and therefore in a limited number of combinations of different Zeitgeber characteristics—, no firm evidence for any of the propositions can be expected. Nevertheless, the likelihood of different contributions to the precision of phasing can be discussed on the basis of the present material.

Ad (1). The seasonal course of variability is quite uniform among the birds (Fig. 26) and among the mammals (Fig. 27). To explain this variability on the basis of changes in the “natural frequency” of the driving oscillation, we have to assume that also these changes in frequency are of uniform type. There is so far little evidence for a seasonal change in freerunning circadian frequency, apart from one case in bats (*Myotis lucifugus*: Menaker, 1961) where differences in physiological state associated with hibernation may have influenced the free-running period, and preliminary observations on fringillid birds (Pohl, unpublished). Among the animals presently studied, the mean phase-angle differences ($\varphi_{\text{midpoint}}$) (Figs. 22 and 24) have revealed no indication of regular seasonal changes in “natural frequency”.

Ad (2). Explaining the seasonal change in precision by Zeitgeber strength one has to assume (a) that a weaker Zeitgeber produces less precise phase control, and (b) that Zeitgeber strength decreases with the approach to the summer and winter solstices.

Weak Zeitgebers may either fail to entrain a circadian rhythm [as demonstrated in a captive woodmouse, *Apodemus flavicollis* in the subarctic summer (Erkinaro, 1969)], produce relative coordination (e.g., as observed in a hamster: Swade and Pittendrigh, 1967), or cause “relative entrainment”. In relative entrainment (described for a mathematical oscillator by Wever, 1971; for the activity rhythm of a flying squirrel, entrained by very short light pulses, by Decoursey, 1962) a phase point of the observed rhythm moves slowly back and forth relative to the Zeitgeber over a number of cycles. Obviously, this phenomenon would add to the day-to-day standard deviation of its phase. Yet, in none of the activity records presently analyzed were such oscillating patterns encountered.

Even without relative entrainment, strength of Zeitgeber may affect precision, although it does not seem to be an a priori necessity. If we assume that there is an effect of Zeitgeber strength on the precision, three different properties of the natural light-dark cycle should be considered as factors possibly determining Zeitgeber strength:

- (a) the range of light-intensities between L and D,
- (b) the duration of twilight, and (c) the L:D ratio (photoperiod).

The strength of a Zeitgeber decreases with its *amplitude*, as has been amply demonstrated for circadian rhythms (Hoffmann, 1969a, b). At the arctic circle, the amplitude of the natural LD-cycle decreases sharply towards the summer solstice, but there is only a weak reduction in midwinter (Fig. 7): because both

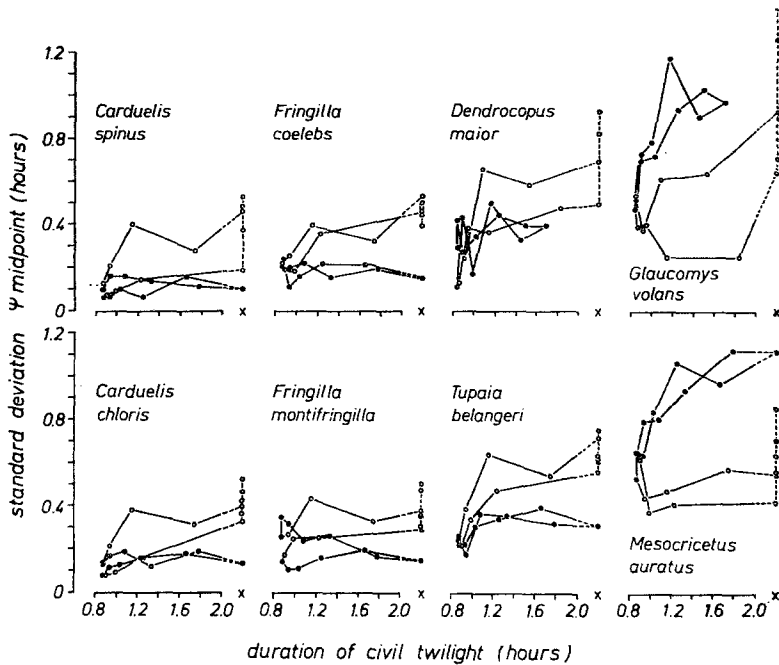


Fig. 28. Variability of ψ_{midpoint} in birds and mammals at the arctic circle as a function of twilight duration. Mean standard deviations from Fig. 26 and 27 plotted as a function of semimonthly mean civil twilight duration. $\circ\cdots\circ$ April–September; $\bullet\cdots\bullet$ October–March; \times civil twilight not defined as the sun does not pass above 0° (in winter) or below -6° (in summer)

at the summer solistice and the winter solistice the sun touches the horizon once, and because the largest changes in light intensity occur when the sun moves between the horizon and 12° below (“nautical twilight”), the LD-cycle in mid-winter is of much larger amplitude than the LD-cycle in midsummer. Night-active mammals, being more sensitive in the low light intensity ranges, would certainly experience a larger Zeitgeber amplitude in midwinter than in midsummer. Yet, their precision is better in summer than in winter (Fig. 27). This can therefore not be explained in terms of amplitude.

The effect of *twilight duration* on the Zeitgeber strength has not been rigorously tested in vertebrates, *i.e.*, no assay of its effect on the range of entrainment or on the amplitude of phase response curves are known. *Twilight duration* undergoes pronounced seasonal changes at the arctic circle. One might suppose a priori that steep changes in light-dark transitions (short twilights) would increase the Zeitgeber strength, but the opposite has also been proposed (Wever, 1967). In Fig. 28, the mean values for the standard deviation of ψ_{midpoint} are plotted as a function of the semimonthly mean duration of civil twilight. The variability increases with longer twilights, so that it would be necessary for Zeitgeber strength to decrease with long twilights in order that the hypothesis be upheld. However, there is a remarkable difference when variability in the winter half (October to March) and in the summer half (April to September) of the year are compared

Table 4. Half months in which maximal precision was observed at the arctic circle, and the corresponding average durations of sunlight

	Species	Half month	Sunlight (hrs)	Mean s.d. ψ_m (hrs)
First half of the year				
Day-active	<i>Carduelis spinus</i>	Mar I	10.7	0.06
	<i>Carduelis chloris</i>	Mar II	12.6	0.07
	<i>Fringilla montifringilla</i>	Feb II	8.9	0.10
	<i>Fringilla coelebs</i>	Feb II	8.9	0.11
	<i>Tupaja belangeri</i>	Mar II	12.6	0.21
Night-active	<i>Mesocricetus auratus</i>	Apr I	14.5	0.37
	<i>Glaucomys volans</i>	Apr II	16.5	0.24
Second half of the year				
Day-active	<i>Carduelis spinus</i>	Oct I	10.5	0.10
	<i>Carduelis chloris</i>	Nov II	4.6	0.12
	<i>Fringilla montifringilla</i>	Dec II	0	0.15
	<i>Fringilla coelebs</i>	Dec II	0	0.14
	<i>Tupaja belangeri</i>	Oct II	8.5	0.18
Night-active	<i>Mesocricetus auratus</i>	Sep I	14.1	0.43
	<i>Glaucomys volans</i>	Sep I	14.1	0.37

(Fig. 28). At seasons of equal twilight duration, the night-active animals are less precise in the winter half of the year, and day-active animals less precise in the summer half of the year. It thus appears that twilight duration cannot be the sole factor involved.

That *photoperiod* has an effect on the Zeitgeber strength is clear from the observation that light-dark cycles with extremely long or short photoperiods lose their entraining capacity (West and Pohl, 1973), and have smaller frequency ranges of entrainment (Wever, unpublished). Little is known of the relationship between these extremes, but it seems reasonable to assume that there is maximum Zeitgeber strength at some intermediate photoperiods, *e.g.*, at LD12:12 (Wever, 1965). Figs. 26 and 27 show that the times of maximum precision occurred in all day-active animals before the vernal equinox and after the autumnal equinox, and in the nocturnal species after the vernal and before the autumnal equinox. The effect of the LD-ratio on Zeitgeber strength, tentatively proposed as the major cause of seasonal fluctuations in precision by us earlier (Aschoff *et al.*, 1972) would require the additional assumption that maximum Zeitgeber strength is not at an L:D-ratio of 1.0, but at values slightly smaller or greater than 1.0 (*cf.* Table 4). It is not unreasonable to assume that the L:D ratio at which the Zeitgeber is of maximal strength depends on the species and is especially different for day- and night-active animals. So far, for such an hypothesis no experimental support exists.

Apparently, the hypotheses dealing with either clock precision or Zeitgeber strength as the major factors in the precision of activity timing seem to require one or more unproven assumptions. No single assumption accommodates the

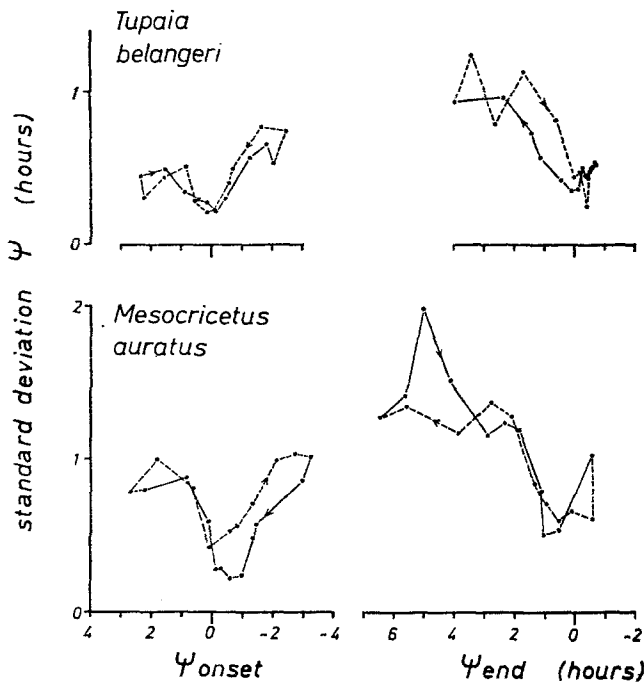


Fig. 29. Variability of ψ_{onset} and ψ_{end} as a function of their mean values in two species of mammals at Messaure. Mean semimonthly standard deviations (ordinate) and mean semimonthly means (abscissa) for January-June (solid lines) and July-December (dashed lines). Arrows indicate the passing of time

differences between species, especially between day-active and night-active animals, and leads to a single coherent explanation of the facts observed.

Ad (3). We have seen that at the arctic circle the times of mean onset and mean end of daily activity cross the times of sunrise and sunset twice a year, or ψ_{onset} and ψ_{end} cross the value zero twice a year, between summer and winter (Figs. 20 and 21). If there were some process involved in the timing of onset and end of activity, making these times most precise when occurring around sunrise and sunset, this would lead to the seasonal variation in precision. Figs. 29 and 30 show that the variability indeed increases when the mean ψ -values are further away from zero. But minimum variability (maximum precision) is apparently not found exactly where the mean ψ is zero. Maximum precision tends to occur when in a day-active animal mean activity onset (night-active: active end) slightly precedes sunrise, and when mean activity-end (night-active: activity-onset) slightly phase-lags sunset. Thus, precision of both onset and end of activity tend to become maximal when means of onset and end fall within civil twilight. This is the part of the day when the rate of change of light intensity is fastest (Figs. 17 and 18). The computed curves of light intensity present the opportunity to estimate the average rate of change of light intensity at the mean time of activity onset and end for every semimonthly interval. The correlation of the

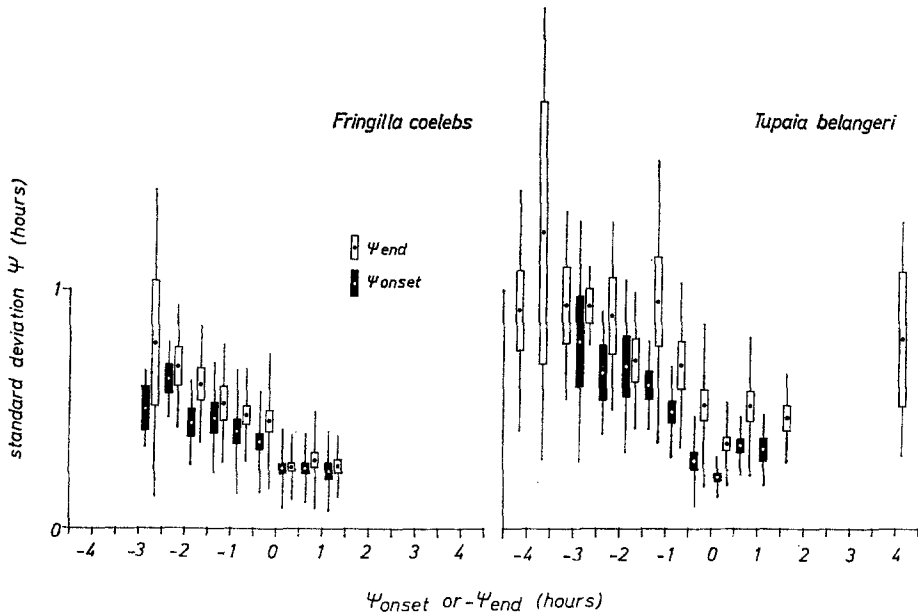


Fig. 30. Mean semimonthly standard deviation of ψ_{onset} (white dots in black bars) and ψ_{end} (dark dots in white bars) calculated in half-hour classes of ψ_{onset} and ψ_{end} for chaffinches and tree shrews at Messaure. The sign of ψ_{end} is reversed (therefore the abscissa labelled: $-\psi_{\text{end}}$) so that the abscissa reads from daytime (left) via sunset/sunrise ($\psi = 0$) to night (right). The vertical lines have a length of 2 standard deviations, the bars have a length of 2 standard errors of the mean

corresponding semimonthly estimate of the precision of activity onset and end with these rates of change ($d\log I/dt$) is shown in Fig. 31 and Table 5. There is always a positive and often a strong correlation between the two parameters. Especially the precision of the end of activity seems to be highly dependent on the rate of change of light intensity at the average time of activity end. Moreover, the precision estimates for a given species from different latitudes seem to lie on different parts of the same regression line.

Considering the hamster and chaffinch results in Fig. 18, we can see how this correlation gives rise to the seasonal variation in the variability of ψ_{midpoint} . In midwinter, the hamsters started activity around 16:00 and stopped around 04:00. Both points, especially end of activity were subject to large day-to-day variations, since the $d\log I/dt$ was minimal at both times, even though at other times of the day steep changes in light intensity were present. Variability decreased until after the vernal equinox, when onsets and ends of activity were at ca. 19:00 and 3:00 and in the civil twilight, i.e., at the largest $d\log I/dt$. In midsummer, activity lasted from ca. 20:00 to 2:00, and was again less precise due to its beginning and termination in almost full daylight, with small $d\log I/dt$. The chaffinches, as birds, have much larger seasonal variation of their activity time than the hamsters: onset and end of activity follow sunrise and sunset more closely, but not completely. In midsummer, activity started at ca. 3:00 and stopped at ca. 20:00, and variability was large due to little change of light intensity at these times of day. With decreasing duration of sunlight, onset and end of activity crossed the time of sunrise and sunset and moved into the civil twilight. Since the activity did not move further into the night, however, and was still within the civil twilight even in

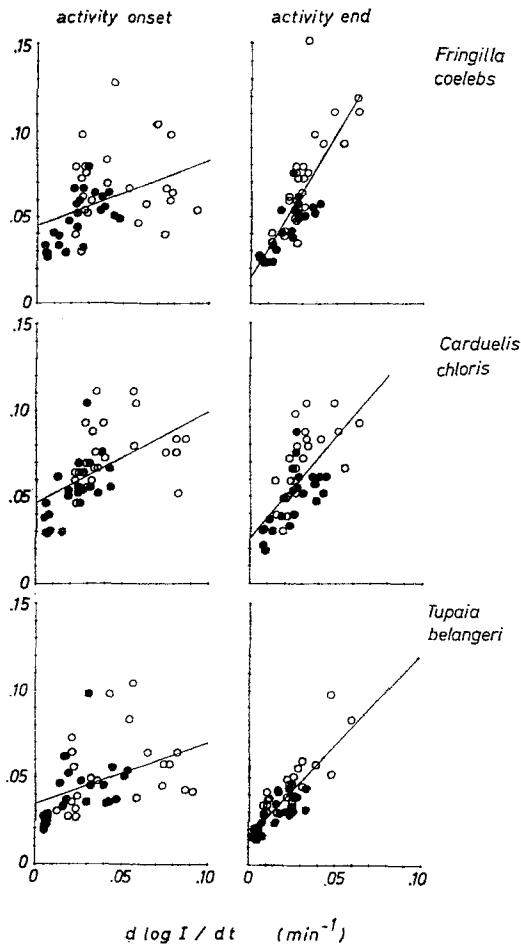


Fig. 31. Precision (1/mean semimonthly standard deviation) of onset and end of activity as a function of the rate of change of light intensity ($d \log I / dt$) at the time of mean onset and end. Values on the abscissa were computed from the slope of daily light curves (see Figs. 17 and 18) at the times of onset and end. Solid dots are 24 semimonthly values from experiments in Messaure, circles are 24 semimonthly values from experiments in Erling-Andechs. Lines are linear regressions. Examples from top to bottom: chaffinch, greenfinch, and tree shrew

midwinter variability did not increase again. Clearly, the existence of a midwinter peak in the mammals, and its absence in birds, is explained by the larger seasonal variation in phase angle difference in mammals (Figs. 20 and 21) than in birds and, relatedly, the smaller seasonal variation in activity time in mammals (Figs. 11–15).

The correlation between precision of onset or end of daily activity and the rate of change of light intensity at those times of day thus seems to lead to a meaningful explanation which accounts for the differences between the seasonal change of precision among species, and for any one species between different latitudes. Elsewhere (Daan, 1975) precision was shown to be experimentally reduced by shifting activity onset and end in chaffinches to times of day with

Table 5. Coefficients of correlation between precision (1/mean s.d.) of time of onset and time of end of activity, and computed rate of change (in log units) of the light intensity at these times. Data from different localities are pooled. Values significantly different from zero ($P < 0.05$) appear in bold type. Number of values used in calculation of the correlation coefficient are given in parentheses

Species	Activity onset	Activity end
<i>Carduelis spinus</i>	0.41 (24)	0.63 (24)
<i>Fringilla montifringilla</i>	0.16 (24)	0.62 (24)
<i>Fringilla coelebs</i>	0.39 (48)	0.79 (48)
<i>Carduelis chloris</i>	0.55 (48)	0.66 (48)
<i>Dendrocopus major</i>	0.33 (28)	0.39 (29)
<i>Tupaja belangeri</i>	0.42 (48)	0.83 (48)
<i>Mesocricetus auratus</i>	0.49 (48)	0.25 (48)
<i>Glaucomys volans</i>	0.64 (48)	0.70 (48)

smaller $d \log I / dt$. In this effect of rate of change of light intensity no property of the driving oscillation *needs* to be involved. This is illustrated by the fact that twilight sensors operated by fixed light intensities show the same correlation between precision and rate of change of light intensities (Section 3) and thereby the same seasonal course of precision (Fig. 10). Obviously, if the mean rate of change of light intensity at a given time of day is large, then the time at which a fixed light intensity threshold is crossed will vary less between bright and overcast days than when $d \log I / dt$ is small. For instance, when $d \log I / dt$ around this threshold is 0.10 min^{-1} , the time at which the threshold is crossed will vary about 10 min between 2 consecutive days with a difference in light intensity of 1 log unit due to meteorological conditions. But when $d \log I / dt$ is 0.02 min^{-1} , the same day-to-day variation will be 50 min. Thus the part of the variability that emerges from rates of change of light intensity may well reflect direct action of light intensity on the observed rhythm rather than precision of resetting the underlying oscillation. A similar conclusion was drawn already (p. 298) from the correlation between ψ_{onset} and ψ_{end} . A possible route of direct effect is given by "masking". In a day-active animal, activity near mean onset and end may be partially suppressed by occasional dark days, or additionally evoked by occasional bright days. The effect would be maximal when the mean $d \log I / dt$ at activity onset and end is minimal. It would yield minimal variability when daily activity is "cut off" by a steep change in light intensity.

In conclusion, the observed daily rhythm of activity appears to be the product of actions of the endogenous clock and of direct responses to light. Lutz (1931), after a month of observations of the onset of morning song in the wren *Troglodytes musculus*, came to the impression that the bird was "a combination of an alarm clock and a photometer". We are inclined to subscribe to his opinion. Had Lutz observed terminations rather than onsets of activity, he might have stressed the photometer more than the alarm clock. Had he brought his bird from Panama to the arctic circle and seen how its onset of morning song would vary over 3 to 4 orders of magnitude of light intensity, he might have rejected the photometer. But at least in the precision as well as in the correlation of ψ_{onset} and ψ_{end} the

photometer still seems to be at work, and it should be emphasized that not all the characteristics of entrained activity rhythms reflect properties of the endogenous circadian oscillation. The general statements which can be based on the present results are:

- (1) Precision of onset and end of activity increases with $d \log I/dt$ at the times of mean onset and end of activity (more markedly for the end of activity).
- (2) If mean ψ_{onsets} and mean negative ψ_{ends} which have the same value (*i.e.* ψ -values derived from onsets and ends recorded at equal distances before sunrise and after sunset) are compared, precision of activity onset turns out to be larger than that of activity end.
- (3) Precision of activity timing is larger in birds than in mammals.

4. General Discussion

4.1. Comparison of the Results with Field Data

There are few generalizations applying to most or all of the species studied. Some seasonal patterns are common to the four fringillid bird species only, and other patterns are apparently species-specific. A maximum in ψ_{midpoint} in the birds' reproductive season is found in all finches (Fig. 22). But there are other seasonal changes in ψ_{midpoint} , unrelated to Zeitgeber properties, which eventually may be explained if more is known about each species.

Before listing the generalizations, some attention will be given to a comparison with data available from animals in natural conditions. For mammals there is little information available on the timing of daily activity in nature. For birds there are comprehensive accounts reviewed by Aschoff and Wever (1962) and Aschoff (1969). Aschoff and Wever (1962) have formulated 6 general rules mainly concerning vocalization and roosting times of birds, as derived from field studies. These can be used as a basis of comparison for the present results obtained in captive animals.

(1) (a) Activity onset in day-active birds is usually at lower light intensities than activity end, (b) in winter the reverse may be true, and (c) the reverse probably holds in night-active birds.

Translated into phase-angle differences, this rule says that ψ_{midpoint} is positive, except in some day-active birds in winter. It was based on a large number of studies compiled and supported by all of the analyses later made by Aschoff (1969). In the present experiments, it was supported in all species (Figs. 22 and 24) except for 3 of the finches (*C. spinus*, *C. chloris*, *F. montifringilla*), which had negative values of ψ_{midpoint} in the arctic midsummer (Fig. 22). Night-active mammals behaved in this regard as expected for night-active birds (Fig. 24).

(2) Species and individuals within a species which start activity early in the day, tend to terminate activity late.

This rule was based mainly on the field studies by Wright (1913) and Mori (1945) involving large numbers of species. The present results, involving a much smaller number of species do not contribute to further *interspecific* evaluation of this rule. With regard to *interindividual* differences, the results from 8 simultaneously recorded siskins give no significant support to the rule.

(3) In day-active birds, males wake up earlier and terminate activity later than females.

The 4 species of finches studied at the arctic circle did not obey this rule, since females in spring and summer had longer activity times (α) than males (Fig. 13). Sexual differences may be species-specific, and they seem of no further relevance to the general principles of circadian rhythms in season and latitude.

(4) Interindividual and day-to-day variations in the time of activity onset are smaller than the variations in activity end.

This rule, based on data from a wide variety of bird species (references in Aschoff and Wever, 1962) is supported by all species presently studied. In view of rule 6, precisions should be compared for onsets and ends of activity occurring at the same light intensity (or solar altitude), or, ψ_{onset} values should be compared with negative ψ_{end} values of the same magnitude.

The examples in Fig. 29 and especially in Fig. 30 show the difference in precision.

(5) The light intensity at activity onset is less subject to (a) seasonal variation and (b) latitudinal variation than the light intensity at activity end.

This implies that ψ_{onset} varies less with season and latitude than ψ_{end} . It is supported by the behaviour of night-active mammals (Figs. 20 and 32) and by some, but not all, of the other species. Activity times in *Dendrocopus major* agree with the rule, both in captive conditions (Fig. 19) and in nature (Aschoff, 1969; Fig. 9).

(6) Interindividual and day-to-day variation in onset and end of activity is smaller on the average when onset and end occur at lower light intensities.

The 5 day-active bird species in the present study all obeyed this rule. The behaviour of the mammals where onset and end of daily activity shifted farther away from sunrise and sunset in the course of the year, leads to the further specification that variability increases again at very low light intensities (Figs. 17, 18, 27 and 29). Precision apparently depends on the rate of change of light intensity rather than on the absolute light intensity (Fig. 31).

Thus, the rules derived from field studies are partly upheld and partly violated by animals in captive conditions. In case of disagreement there seem to be species differences in the patterns observed. There is no a priori reason to assume systematic differences in the timing of activity for free living animals and for animals kept in captivity. However, such differences may exist (e.g. Dunnett and Hinde, 1953; Råber, 1949; Kenagy, 1975) whether due to differences in light intensities experienced by the animals, to differences in climatic conditions (indoors versus outdoors), to differences in the physiological state of the animals related to general living conditions, or due to differences in the assays used to record the activity rhythm. If they exist, they very well may have a bearing on the conclusions drawn.

The remaining generalizations that can be made for both field data and experimental results in conditions of natural daylight are:

(1) With longer photoperiods, activity in day-active animals starts earlier in local time, but later relative to sunrise (ψ_{onset} smaller), and terminates later in local time, but earlier relative to sunset (ψ_{end} larger). The reverse holds in night-active animals. The resulting S-curve of activity time as a function of photo-

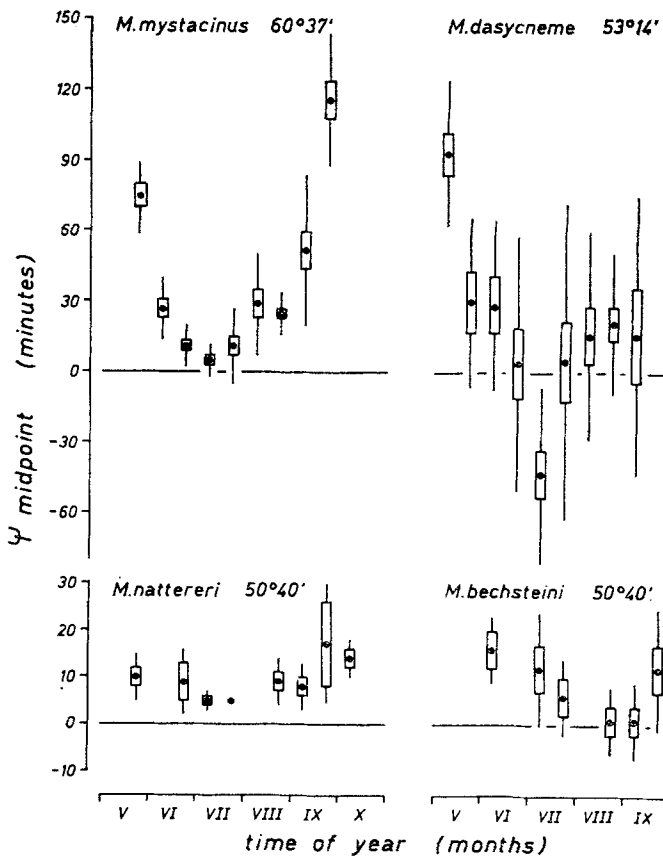


Fig. 32. Seasonal change in phase-angle difference (ψ_{midpoint}) in four species of bats of the genus *Myotis*. Calculated from field data by Nyholm (1965, Fig. 36: *M. mystacinus*), Voûte (1972, Fig. 20: *M. dasycneme*) and Laufens (1972, Fig. 6, 30: *M. nattereri* and *M. bechsteini*)

period with a slope significantly less than 1.0 is characteristic of *all* animals studied in natural (Aschoff, 1969) and in captive conditions.

(2) Onset and end of activity follow sunrise and sunset more closely in birds than in mammals. Seasonal variation in ψ_{onset} and ψ_{end} is thereby smaller in birds than in mammals, and seasonal variation in α is larger in birds than in mammals. Day-to-day variations in the times of activity onset and end are larger in mammals than in birds.

(3) As a tendency rather than a strong generalization, we can state that onset of activity is usually more precise than activity end, its precision less affected by day-to-day variations in light intensity, and in the course of the year tends to stay closer to sunrise (day-active animals) or sunset (night-active animals).

4.2. Implications for Models of Circadian Activity Rhythms

An S-shaped relationship between activity time and photoperiod, produced by opposite seasonal changes of ψ_{onset} and ψ_{end} (Figs. 11–15) is the most important

one of the 3 generalizations formulated in the previous section, and any model of the formal structure of circadian oscillations will be adequate only if it accommodates this phenomenon. In the level-and-threshold model of circadian rhythms of activity (Wever, 1965) the duration of α is determined by the time the oscillation stays above a threshold. As can be derived from computer simulations of the entrained model oscillation (*e.g.* Wever, 1964; Fig. 7), the dependence of α on photoperiod is, for some combinations of factors, in principle similar to that observed in the species discussed here.

Another approach to the problem starts from the fact that daily onset and end of activity move in opposite directions with changes in photoperiod (Figs. 20 and 21), as well as with changes in the intensity of illumination (Daan, 1975); this can be interpreted as reflecting two systems with different responses to light, although it would not be compulsory evidence. The existence of two oscillating systems involved in the circadian rhythm of activity is further suggested by its usually bimodal pattern (Aschoff, 1962). With increasing activity time, the two peaks move apart (Aschoff, 1966), *i.e.*, they stay closer to activity onset and activity end than to each other; the opposite would be expected if there were one oscillation with varying level. The most suggestive indication of *two* oscillations is the phenomenon of "splitting" of circadian rhythms of activity, a process in which two components freerun for some time with different circadian frequencies. This has been observed in several species of mammals (Pittendrigh, 1960, 1967; Hoffmann, 1970, 1971; Pohl, 1972) and recently in birds (Gwinner, 1974).

To account for both splitting and bimodality, Pittendrigh (1974) following earlier suggestions (Gwinner, in Aschoff, 1967; Hoffmann, 1967) has proposed a two-oscillator system as the basis of circadian rhythms of activity: A morning oscillator (M), which is speeded up by light, and thereby tends to lock on to dawn, and an evening oscillator (E; Pittendrigh's night oscillator N) which is slowed down by light and thereby tends to lock on to dusk. Activity onset would be linked to E in night-active animals, and to M in day-active animals, and activity end linked to M in night-active and to E in day-active animals.

If there are really two oscillators involved, they must be coupled either mutually or unilaterally, since in free-running conditions they share a common frequency, except in the phenomenon of splitting. Coupling means that there is some force at work to keep the two oscillators in a certain phase relationship to each other. On the other hand, locking on to dawn and dusk by the two oscillators would imply that in the course of the year, when sunrise and sunset move apart, this phase relationship changes. The coupling force between the oscillators must then necessarily counteract the coupling of each of them to dawn or dusk. One would expect this counteraction to increase when the two oscillators are pulled further away from their "natural" phase relationship, *i.e.* with extremely long and extremely short days as occur in the arctic summer and winter. Since activity onset and activity end are assumed to be phase points of the two oscillators, the interval (α) between them would be a measure of their mutual phase relationship. Thus, if we assume an internal coupling force counteracting the effects of changing photoperiod and keeping the phase relationship within certain limits, the smooth S-shaped curve of α as a function of photoperiod is readily explained.

The slight differences in the variation of activity onset and activity end with season and latitude (generalization 3) are compatible with the one- as well as with the two-oscillator model. In the two-oscillator model, we could accommodate the facts that activity onset is usually less subject to day-to-day variation, is less affected by external influences, and stays closer to dawn or dusk than the end of activity, by assuming that the oscillation to which activity onset is coupled is of larger amplitude and perhaps "dominates" over the activity-end oscillator. The common "bigemini" (Aschoff, 1962), a pattern of daily activity with one large peak followed by a small peak, suggests such a possibility. Then in a night-active mammal the E-oscillator would be dominant, and in the day-active birds the M-oscillator would be dominant.

We would expect changes in the α/ρ ratio to accompany changes in the period τ of the free running rhythm when the latter are brought about by changes in the intensity of constant illumination. For instance, in a day-active bird an increase in light intensity would cause a decrease in the natural period of the morning oscillator (τ_M) and an increase in τ_E . Since the phase relationship between the two oscillators ($\psi_{M,E}$) which in day-active birds equals α , increases with the ratio τ_E/τ_M , α will increase with light intensity. In night-active mammals, where $\psi_{M,E} = \rho$, ρ will increase (and therefore α decrease) with light intensity. This is experimentally known (Aschoff, 1960).

Thus, the two-oscillator model seems to combine the major empirical facts concerning circadian rhythms of locomotor activity both in conditions of free-run and of entrainment by natural light-dark cycles. It may eventually give an explanation for the seasonal inversion of activity rhythms known in microtine rodents (Ostermann, 1956; Erkinaro, 1961) and salmonid and cottid fishes (Kalleberg, 1958; Müller, 1968, 1970; Eriksson, 1973) where otherwise day-active animals become night-active in summer. This phenomenon may turn out to be related to "splitting" in free-running rhythms (Hoffmann, 1971) where apparently two distinct stable phase relationships, about 180° apart, can be realized.

The problem of parametric versus non-parametric modes of entrainment would not be different for one-oscillator and two-oscillator systems. The question remains open whether changes in light intensity rather than absolute light intensities are the major agents involved in entrainment. In constant illumination, *differential* effects are, by definition, excluded. The fact that in many animals the free-running period (τ) changes with light intensity is, therefore, proof of the existence of *proportional* effects of light on the system. On the other hand, the phase shifts caused by single short light pulses in otherwise constant darkness are clear expressions of the differential effect of a Zeitgeber. The magnitude of such phase shifts suggests that differential effects can be major constituents in the process of entrainment. The involvement of photoreceptors adapting to levels of constant illumination is one possible source of sensitivity of the circadian pacemakers to changing rather than to constant light intensities.

The night-active mammals investigated so far largely obey the "seasonal rule" in having larger values of ψ_{midpoint} in winter than in summer. Aschoff (1964) has explained this rule by assuming that proportional effects of the light-dark cycle were such that longer days involve a higher average light intensity, and thereby decrease the natural circadian frequency in night-active animals, which—in conditions of entrainment—would lead to a smaller (less positive or more

negative) phase-angle difference in summer. An analysis of data from several recent studies on the daily timing of foraging activity in bat colonies (Fig. 32), suggests that the seasonal rule applies to natural situations, too. The habit of these species of bats to hide in dark roosts in daytime make it improbable that proportional effects of light are involved here. The colony of pond bats (*Myotis dasycneme*) investigated by Voûte (1972), for instance, was located in the loft of a church where no daylight penetrated. The animals woke up in the late afternoon in the colony, and one after the other moved to a "waiting room", a space near the exit of the loft, where daylight was perceptible, for less than 1 hr before the majority of bats took off almost simultaneously. There was no indication of more time spent in this "light-sampling behaviour" (Twente, 1955) in summer than in spring or autumn. The seasonal differences in phase-angle differences (Fig. 32) can, therefore, not be explained by proportional effects of the average light intensity over 24 hrs.

In terms of the two-oscillator model (Pittendrigh, 1974), the validity of the seasonal rule for all night-active mammals for which data were obtained either in the field or in captivity, again suggests that the oscillator governing onset of activity is generally dominant over the oscillator governing end of activity. Activity onset locks closely onto sunset, and seasonal variations in ψ_{onset} are smaller than in ψ_{end} . Seasonal variation of their average, ψ_{midpoint} , then largely reflects variations in ψ_{end} , which are characterized by a minimum in summer in night-active mammals.

The analysis of all the data accumulated does not allow a decision between the one- and the two-oscillator model. Several of the generalizations are compatible with both of them. However, at least the predictions from the one-oscillator model concerning the seasonal course of ψ_{midpoint} (Figs. 22 and 24) and its correlation to α (Table 2) are not matched by the data. On the other hand none of the generalizations contradicts the two-oscillator model.

4.3. Birds versus Mammals

As stated above (generalization 2), the circadian activity pattern follows seasonal and latitudinal variations in photoperiod more closely in birds than in mammals. The precision of the avian rhythms is usually larger than that of the mammal rhythms. There are other differences, perhaps related to these: after a phase shift of the light-dark cycle, activity rhythms of birds become resynchronized faster than those of mammals (Hoffmann, 1969a). The minimum amplitude of the light-dark cycle necessary for entrainment is smaller in birds than in mammals (Hoffmann, 1969a). Phase response curves for light pulses seem to have larger amplitude in birds (Eskin, 1971; V. Saint Paul, unpublished) than in mammals (DeCoursey, 1960, 1964; Pittendrigh and Daan, 1975), although the differences between the techniques used obstruct rigorous comparison. The change in intensity of continuous illumination appears usually to have stronger effects on the free-running circadian period in birds than in mammals (Aschoff, 1965). There are major differences in the physiological organization of the avian and mammalian circadian system, e.g., in the participation of the pineal organ and of extraocular photoreceptors in entrainment of the rhythms

(Menaker, 1974). How these differences are related to the differences in the activity rhythms as influenced by season and latitude remains to be revealed.

Further, the question can be raised, whether there is biological meaning to a difference in sensitivity of the avian and mammalian circadian system to light as the major entraining agent. The answer is in no way clear if locomotor activity is considered. Apart from adjusting activity, and other biological functions, to the temporal order of the environment, circadian clocks play an important role in photoperiodic time measurement. One of the mechanisms proposed for the measurement of photoperiod is "internal coincidence" (Pittendrigh, 1972; Gwinner, 1973). It postulates two circadian oscillations with a mutual phase relationship subject to seasonal fluctuations. It is tempting to speculate that such oscillations, whatever their physiological nature, would have similar phase relationships to dawn and dusk in the course of the year as activity onset and activity end. Their internal phase relationship (ψ_i) would, then, undergo the same seasonal variation as the activity time.

If a system were available where photoperiod can be measured via its effects on the phase relationship between oscillations (ψ_i) one would expect that any selective pressure for precise measurement of photoperiod would favour large seasonal variations and small day-to-day variations in ψ_i . Both properties are found in the circadian activity rhythms of birds, as contrasted to mammals. Most birds of the temperate zones probably utilize photoperiod for the recognition of season. In mammals photoperiodic reactions are far less marked. Menaker (1971) has recently suggested that "in mammals much of the pressure for precise synchronization of reproductive activity with season may have been removed by the evolution of the mammary glands, which enable the female to provide nourishment for the young from a wide variety of nutrient substrates. It would therefore not be surprising that photoperiodic control were less general and less rigorous among the mammals than among birds". If the circadian rhythm of activity indeed somehow reflects the circadian system involved in photoperiodic time measurement, such considerations may be a guide to functional aspects of seasonal and daily variations in the timing of daily activity.

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